WAVE FORM AND GONOPOD SHAPE IN SYMPATRIC SPECIES OF UCA

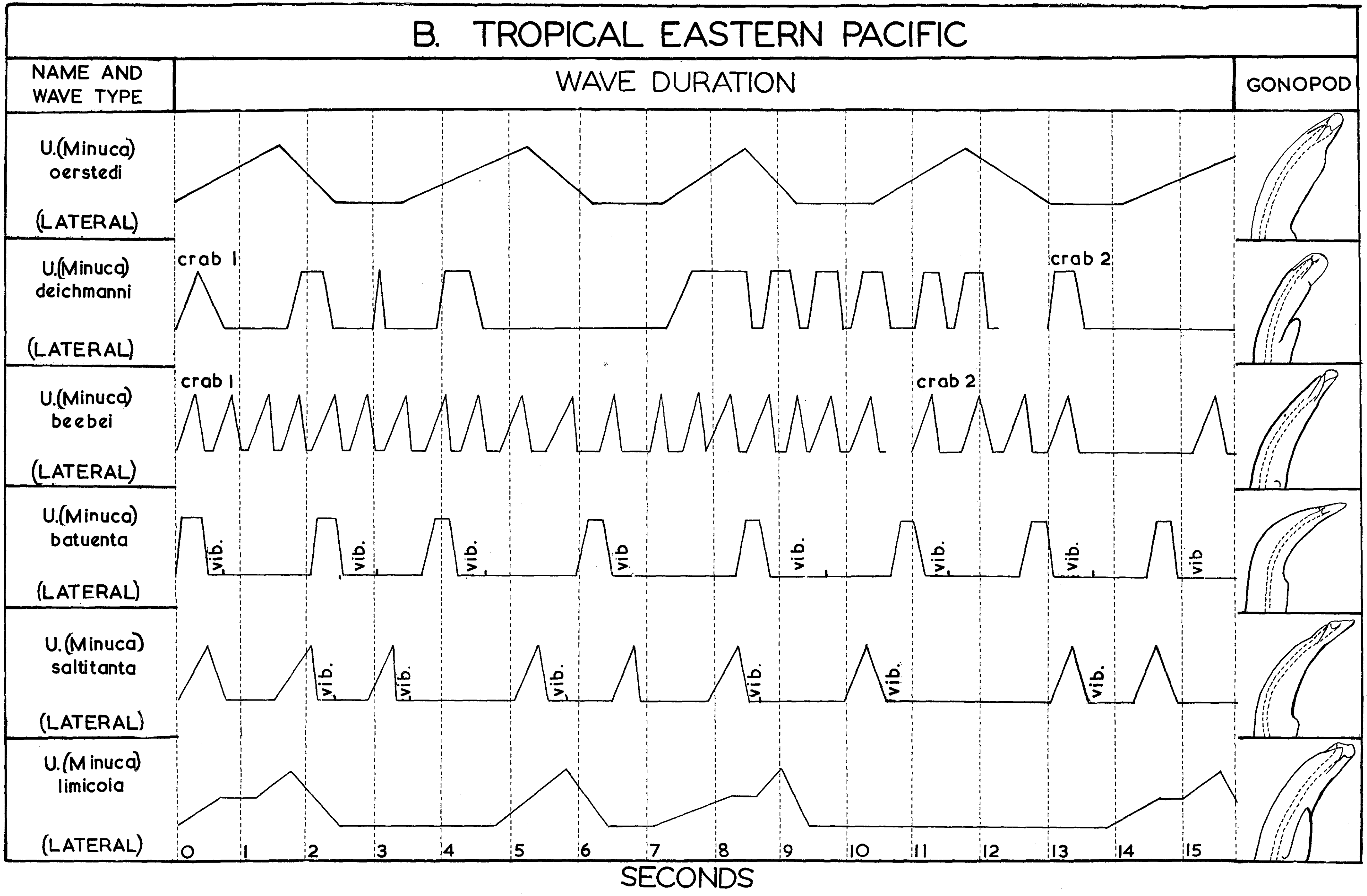
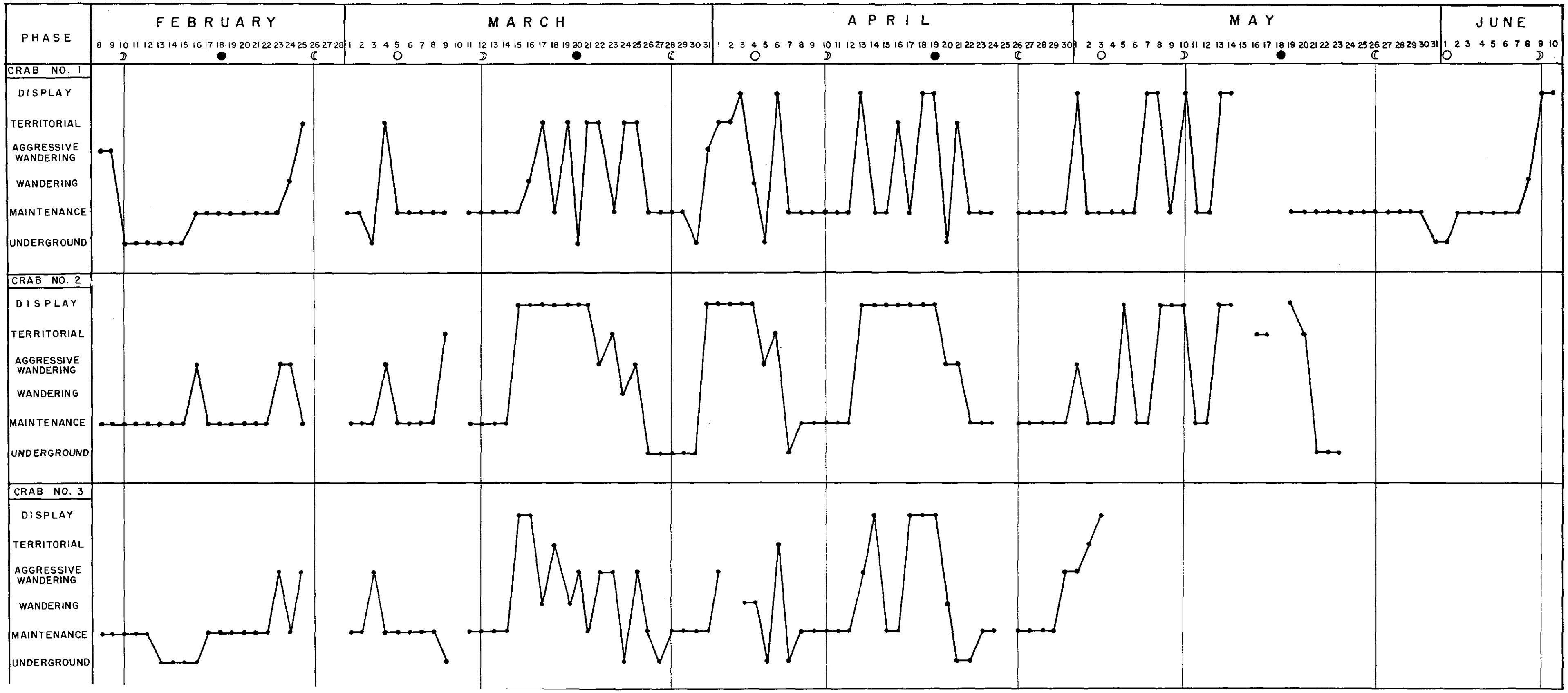
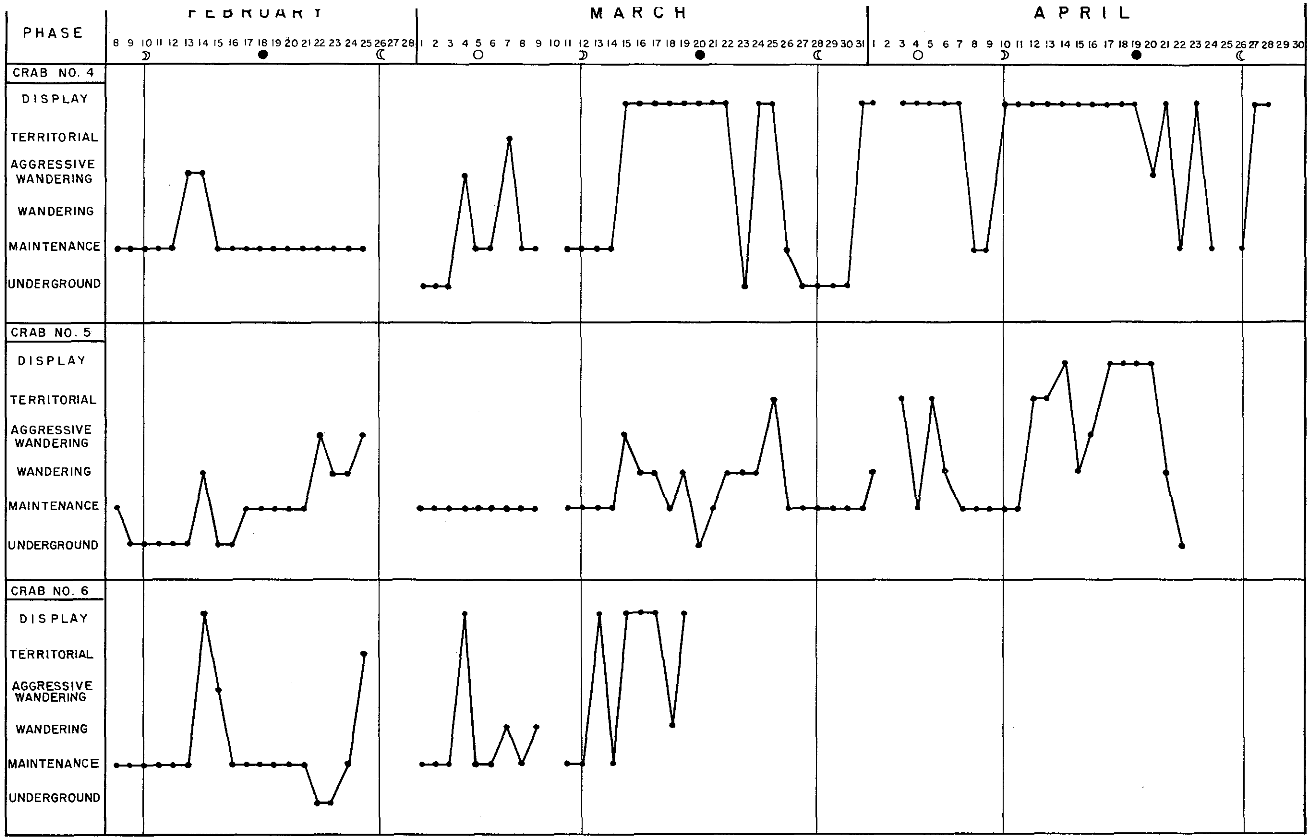


FIG. 93. Wave form and gonopod shape in sympatric species of *Uca*. From films made in the tropical eastern Pacific, near Old Panama, R.P. Since all these species are members of the subgenus *Celuca*, they are rather closely related. Only three, *oerstedi*, *batuenta*, and *saltitanta*, share so many characteristics that they merit the term "closely sympatric." When the cheliped is held in place briefly at a wave's peak, the pause is indicated in the diagram by a plateau. "VIB": vibration, the strokes being too rapid to show individually on motion picture film, exposed at speed of 1/48 sec. (24 frames per sec.). (Pp. 528ff.)

FIG. 94. Activity phases of *Uca* (*Uca*) *maracoani maracoani* in an outdoor crabbery. Phase sequences in behavior of six adult males. The position of each dot indicates the highest types of activity attained by an individual on a particular date, when these types are arranged in a series from least social to most social. The complete natural sequence appears to range from uninterrupted inactivity underground, through simple maintenance (feeding and digging) activities, wandering, aggressive wandering, territoriality, and, finally, display. Gaps in the diagrams represent days when observations were missing or inadequate. The graph of each individual's activity ends with the day before its death. These specimens were selected for illustration because of their longevity. The shorter records of fifteen other individuals showed similar characteristics. (Pp. 505ff.)

94





95

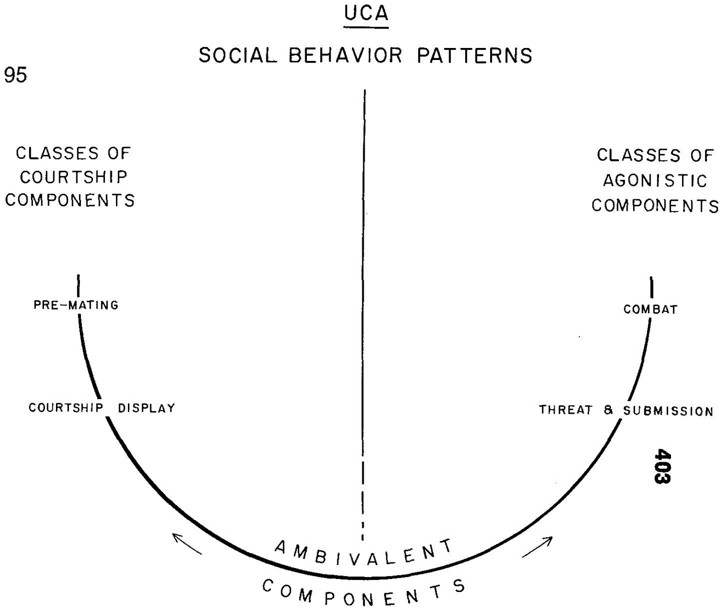


FIG. 95. Diagram indicating the extent of ambivalence in social behavior patterns in *Uca*. (Pp. 517ff.)

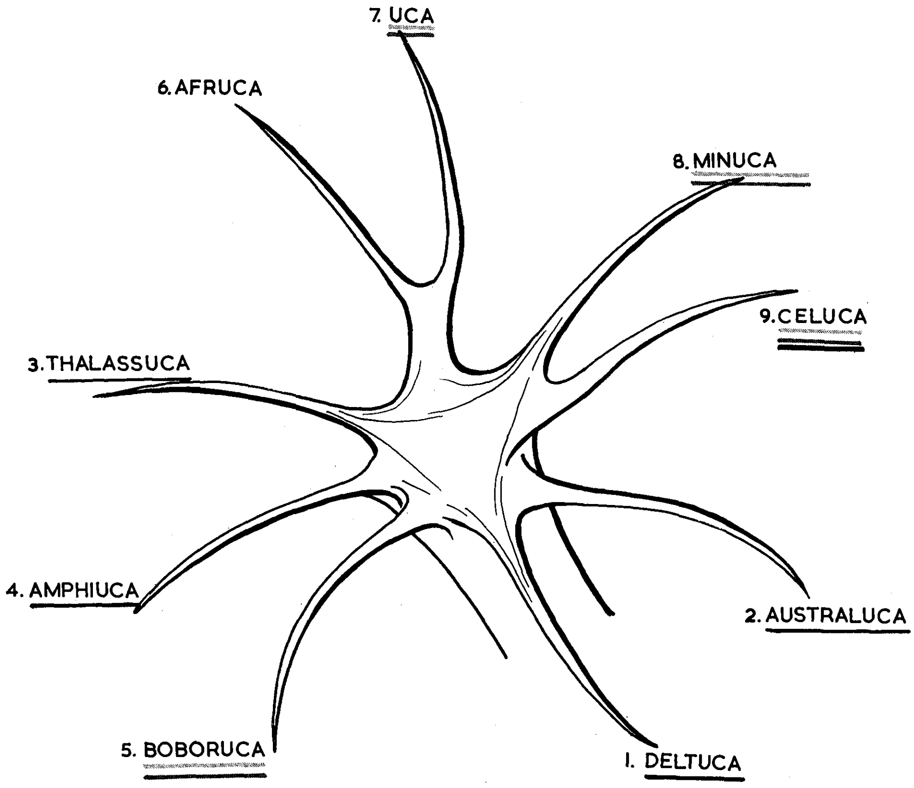


FIG. 96. Dendrogram: subgenera of *Uca*. Key to underscoring of names: black, occurs in the Indo-Pacific; pale gray, eastern Pacific; dark gray, western Atlantic. (Pp. 18, 531.)

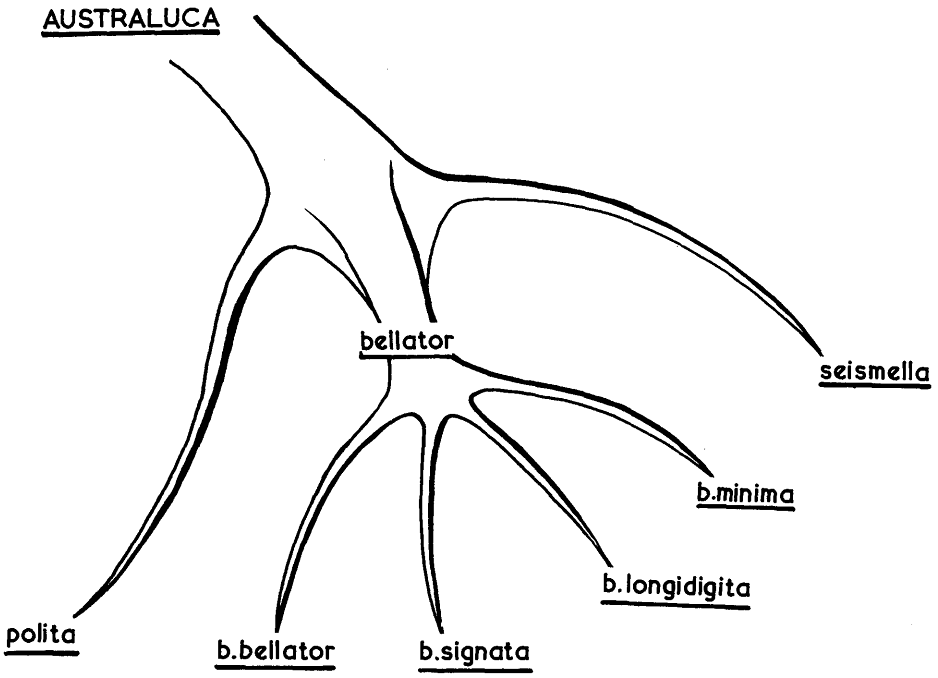


FIG. 97. Dendrogram: subgenus *Australuca*. Key to underscoring as in Fig. 96. (Pp. 63, 531.)

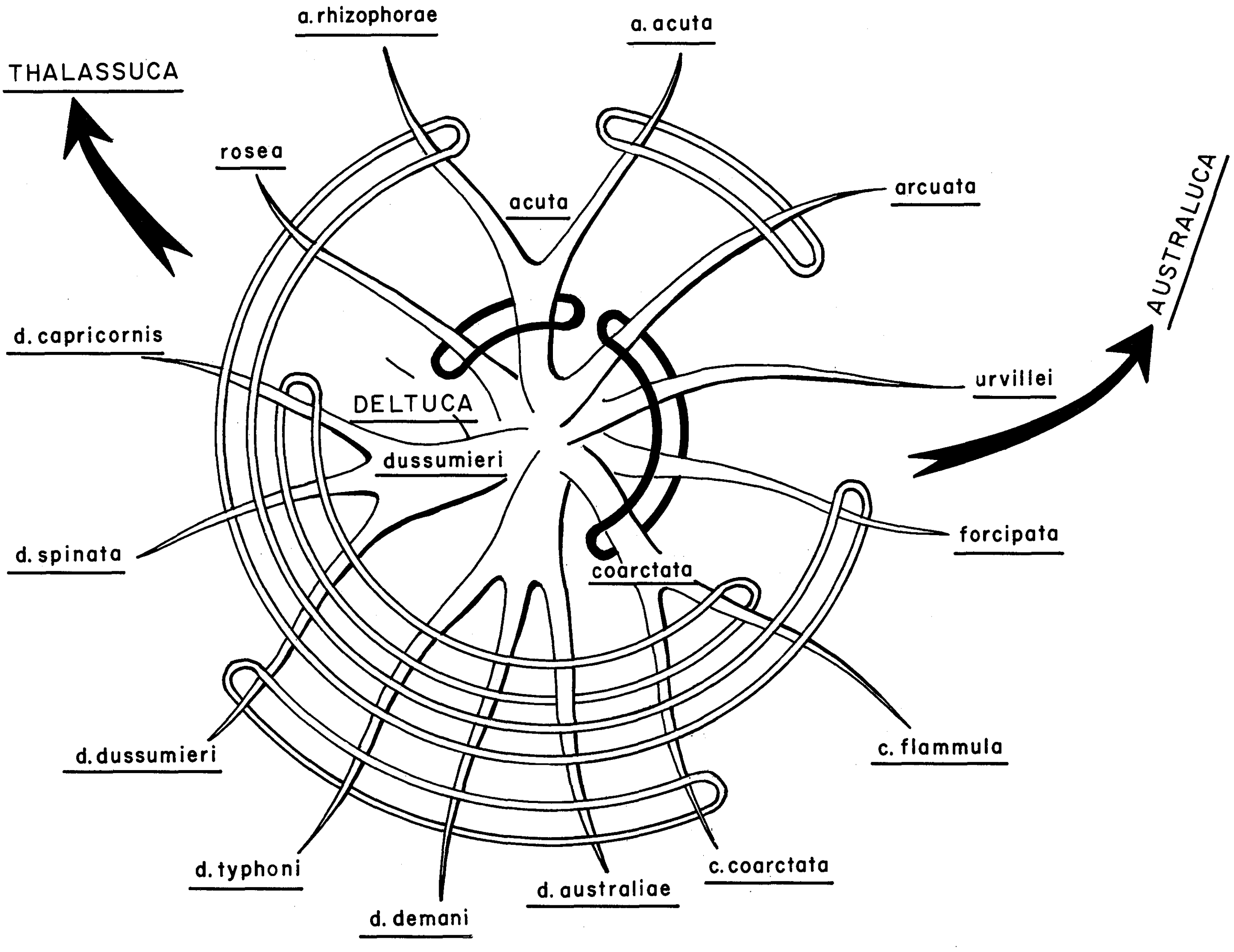


FIG. 98. Dendrogram: subgenus *Deltuca*. Black bands, superspecies. Hollow bands, sympatric forms; exception: *demani typhoni* and *demani demani*, which replace each other allopatrically. Key to underscoring as in Fig. 96. (Pp. 24, 531.)

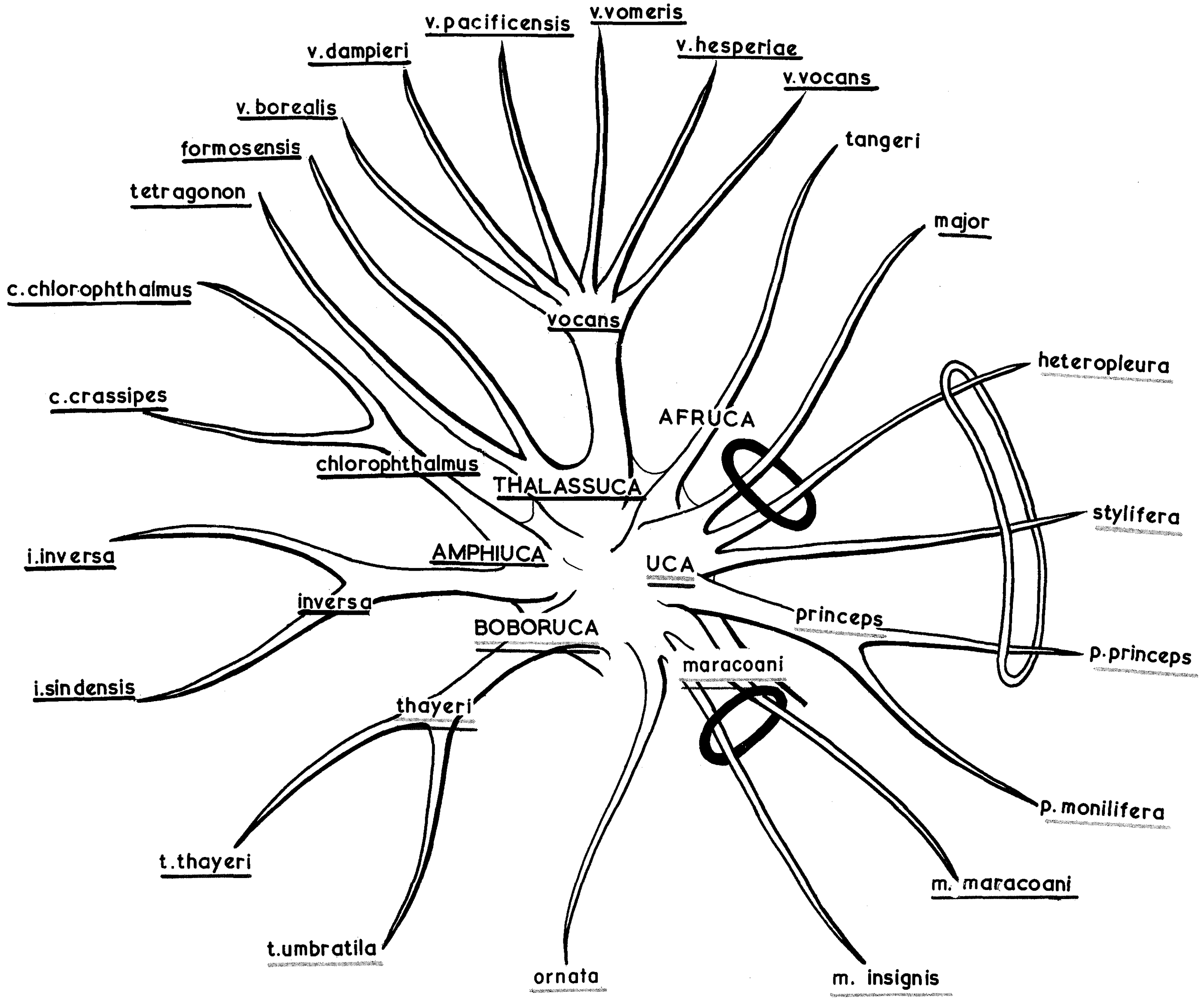


FIG. 99. Dendrogram: subgenera *Thalassuca*, *Amphiuca*, *Boboruca*, *Afruca*, *Uca*. Key to underscoring as in Fig. 96. Black bands, superspecies. Hollow bands, sympatric forms. Key to underscoring as in Fig. 96. (Pp. 76, 97, 111, 117, 127, 532.)

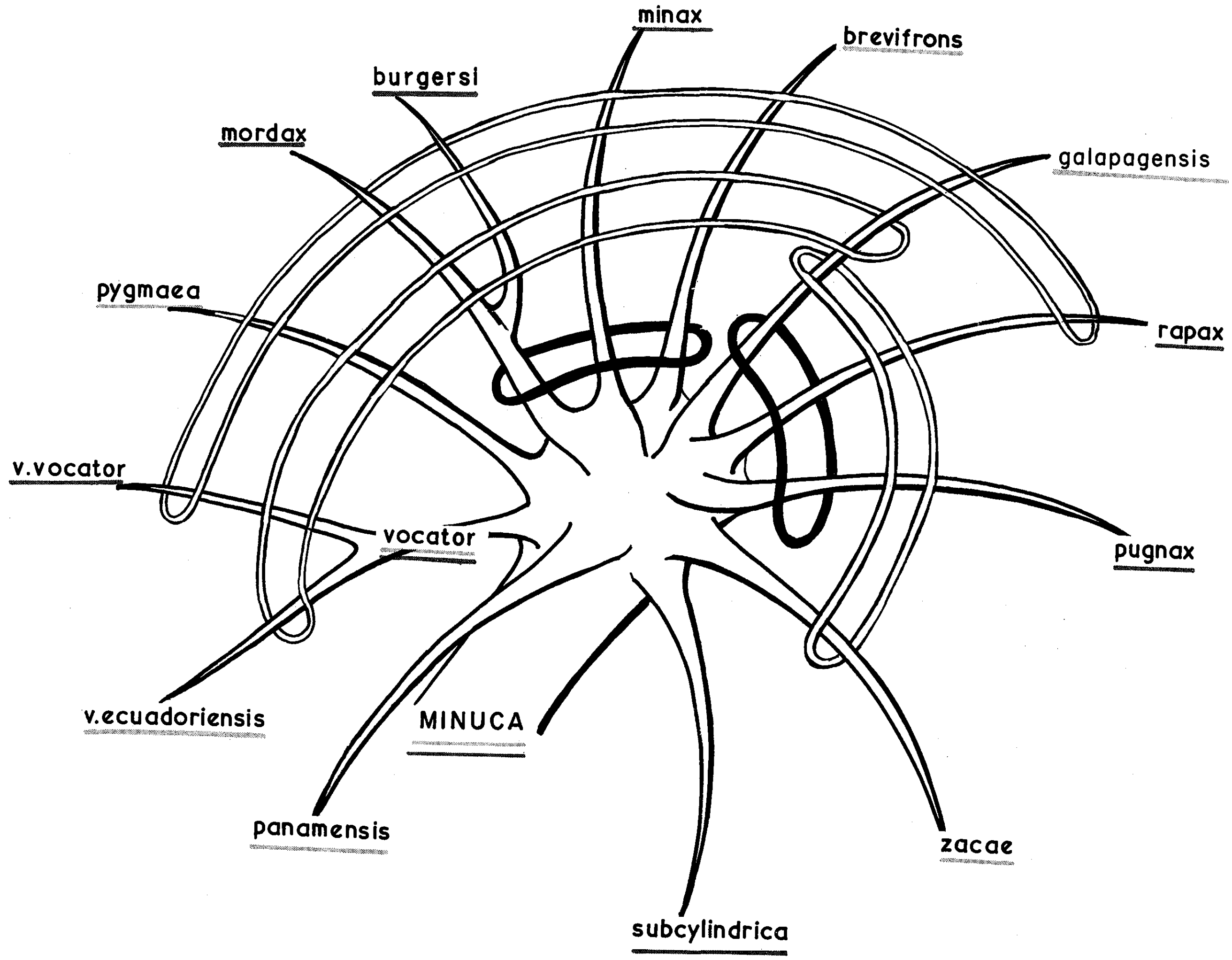


FIG. 100. Dendrogram: subgenus *Minuca.* Black bands, superspecies. Hollow bands, sympatric forms. Key to underscoring as in Fig. 96. (Pp. 156, 533.)

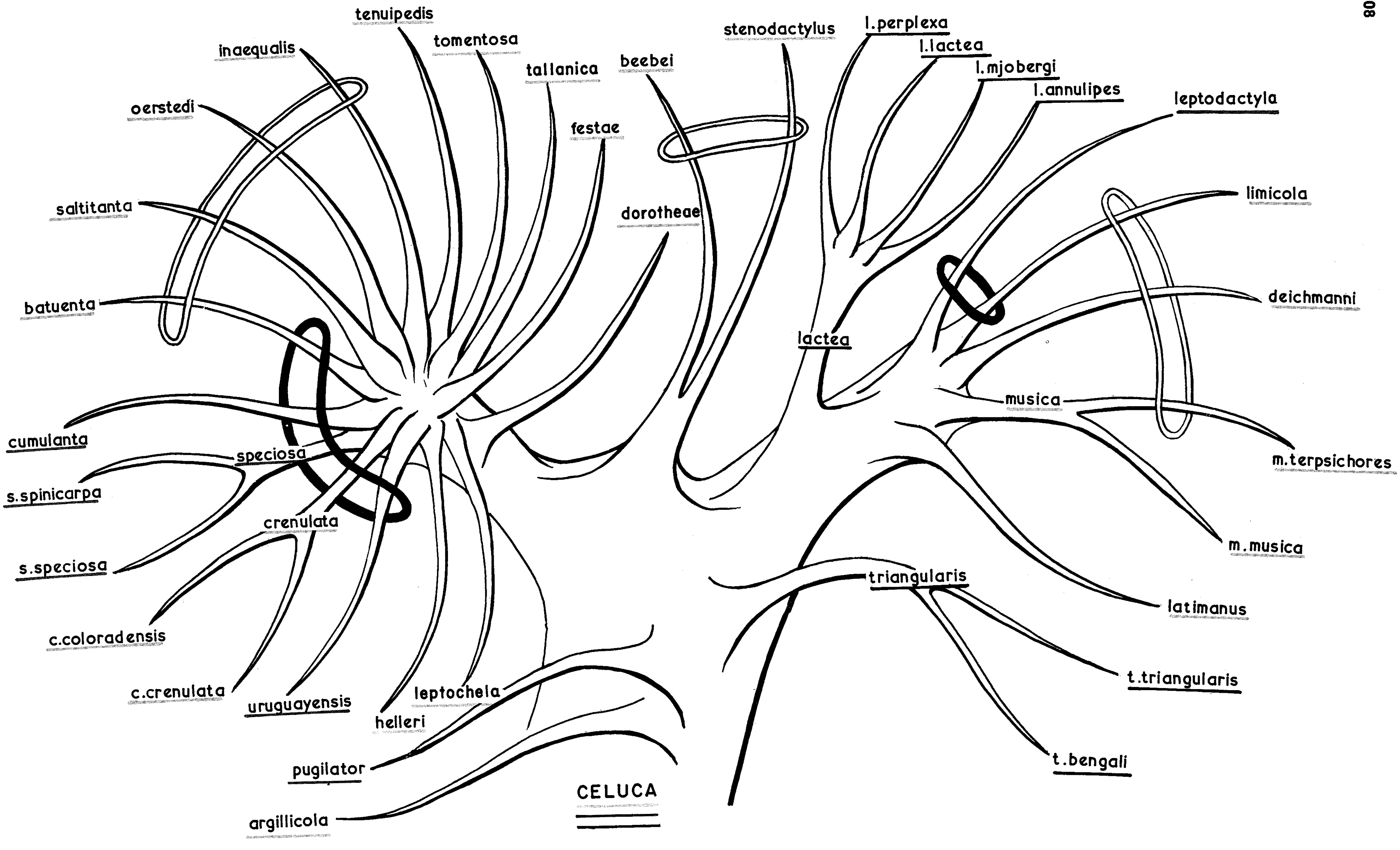


FIG. 101. Dendrogram: subgenus *Celuca*. Black bands, superspecies. Hollow bands, sympatric forms. Key to underscoring as in Fig. 96. (Pp. 217, 533.)

Maps

INTRODUCTION

The 21 maps that follow consist of 17 in black-and-white and four (nos. 18-21) partly in color.

The first illustrates the distribution of the genus *Uca*, along with degrees of concentration of its species.

Numbers 2-17 show the distribution of most of the species, usually arranged in the sequence of subgenera employed in this contribution. Because of the prevalence of sympatry, however, and the exigencies of photoreproduction, many species are not presented in taxonomic sequence. In particular, the last maps, nos. 18-21, follow the American series, but show, with the aid of color, the complex distribution of certain Indo-Pacific forms that are taxonomically scattered.

To aid rapid comparison of ranges, an alphabetical list of species with corresponding map numbers follows this introduction.

Screens. Throughout the series the extent of each screen represents my conclusion on the probable distribution of the species at the present time, based on information that appears to me to be reliable. This information consists first of published records which seem to me trustworthy, either because the contribution is the work of an experienced specialist, or the record of a species in a part of its range where it is otherwise known to occur, or because I have examined the material in the museum where it is deposited. Second, the ranges are based on additional specimens in museums which have never been recorded in print, or for which references to the published accounts were not certainly determined, if at all. The third source of information is provided by specimens I collected in the field (Table 24).

Records that seem to me wholly erroneous, such as the occurrence of a species in Odessa or Yugoslavia, have been omitted from the maps, although they are discussed under the species concerned and listed in the section on questionable geographic records (p. 326). Where boundaries are uncertain because of the absence of recent records, as in Chile, the screen ends with an irregular edge; where records are wholly lacking throughout a wide area between populations, the sections of screen are rounded off.

Symbols. For all the Indo-Pacific species dots and other symbols mark the localities where specimens that I have personally examined were collected. On maps where a number of such localities are very close together, as on the northwest coast of the Gulf of Davao, a single dot represents two or more sites. In some older museum specimens the label gives only a general locality, such as "Japan" or "Madagascar." If I did not find material to examine from particular localities in the same area, I used an open diamond symbol on the map; otherwise the more general name is not represented. An arrow indicates an extension of a range beyond the confines of the map.

Of special interest on Maps 18-21 are the colored symbols falling outside the usual boundaries of the species or subspecies, within the range of an allopatric form. These distributions are discussed under the species headings in the systematic section, in Chapter 1 and in Chapter 7; see also Tables 3, 6, and 22.

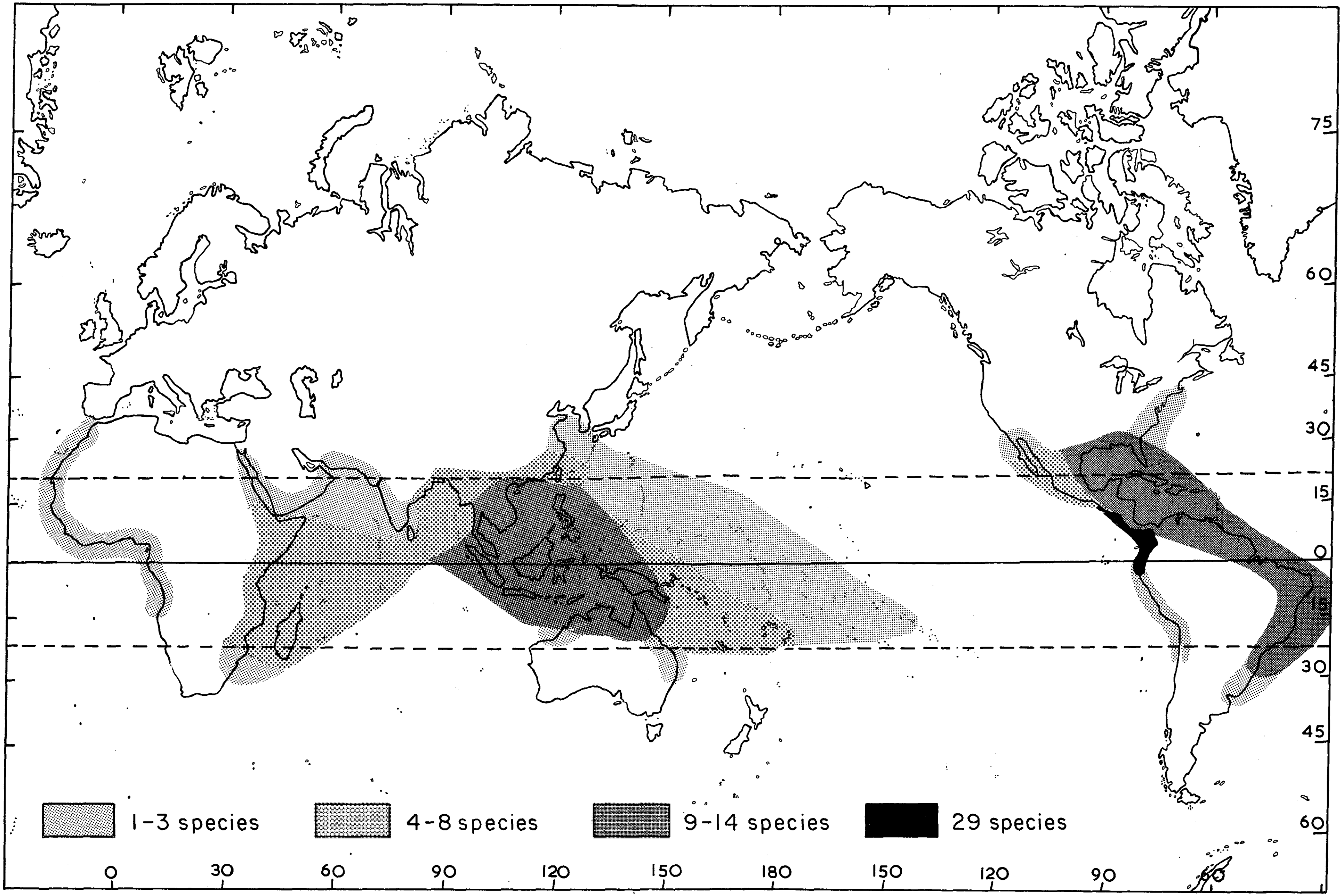
No symbols appear on any American map, since they proved in some cases to be impractical because of extensive sympatry and in all to be of doubtful value. These numerous American forms are usually characterized by short or narrow ranges in uncomplicated patterns, while their taxonomic histories are, with a few famous exceptions, less tortuous than those of most Indo-Pacific species. It seemed, therefore, that on American shores the precise localization on a crowded map of the origins of examined specimens would not be very helpful, either in clarifying allopatric situations or in evaluating evidence for particular distributions.

All of the records of material examined, both precisely and imprecisely localized, are listed in Appendix A. Ranges of the species and subspecies appear under appropriate headings in the systematic section. The chapter dealing with zoogeography starts on p. 431.

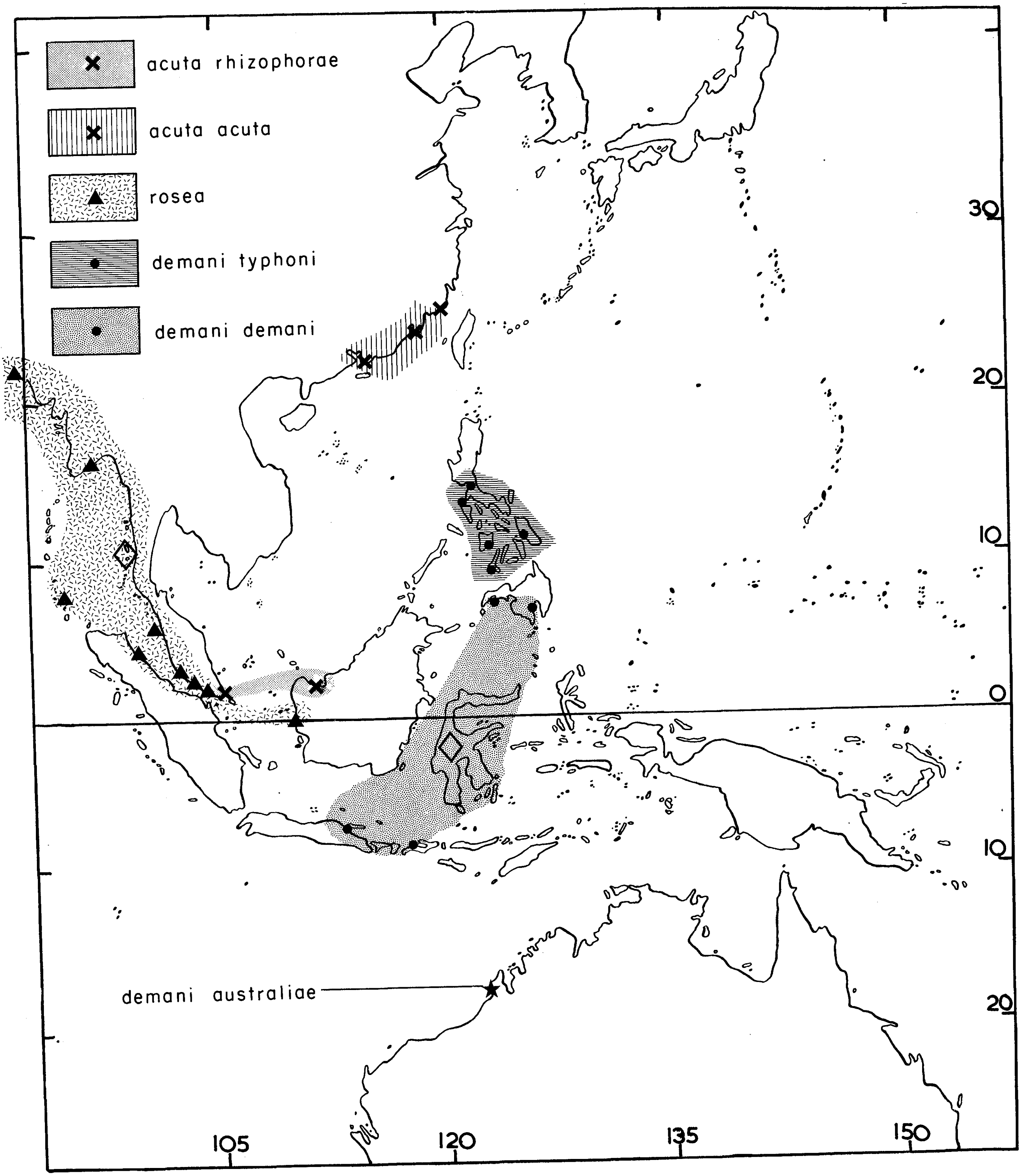
Excluded from the maps and from Appendix A is museum material I examined early in the course of the study before I had attained sufficient knowledge of the forms involved to refer them with confidence to species or subspecies. This limitation applies particularly to the collection of Australian material in Sydney. The indicated ranges of some species occurring in Australia are, therefore, almost certainly already in need of extension.

Alphabetical List of Species of the Genus *Uca*, with Number of Map on Which Each Appears

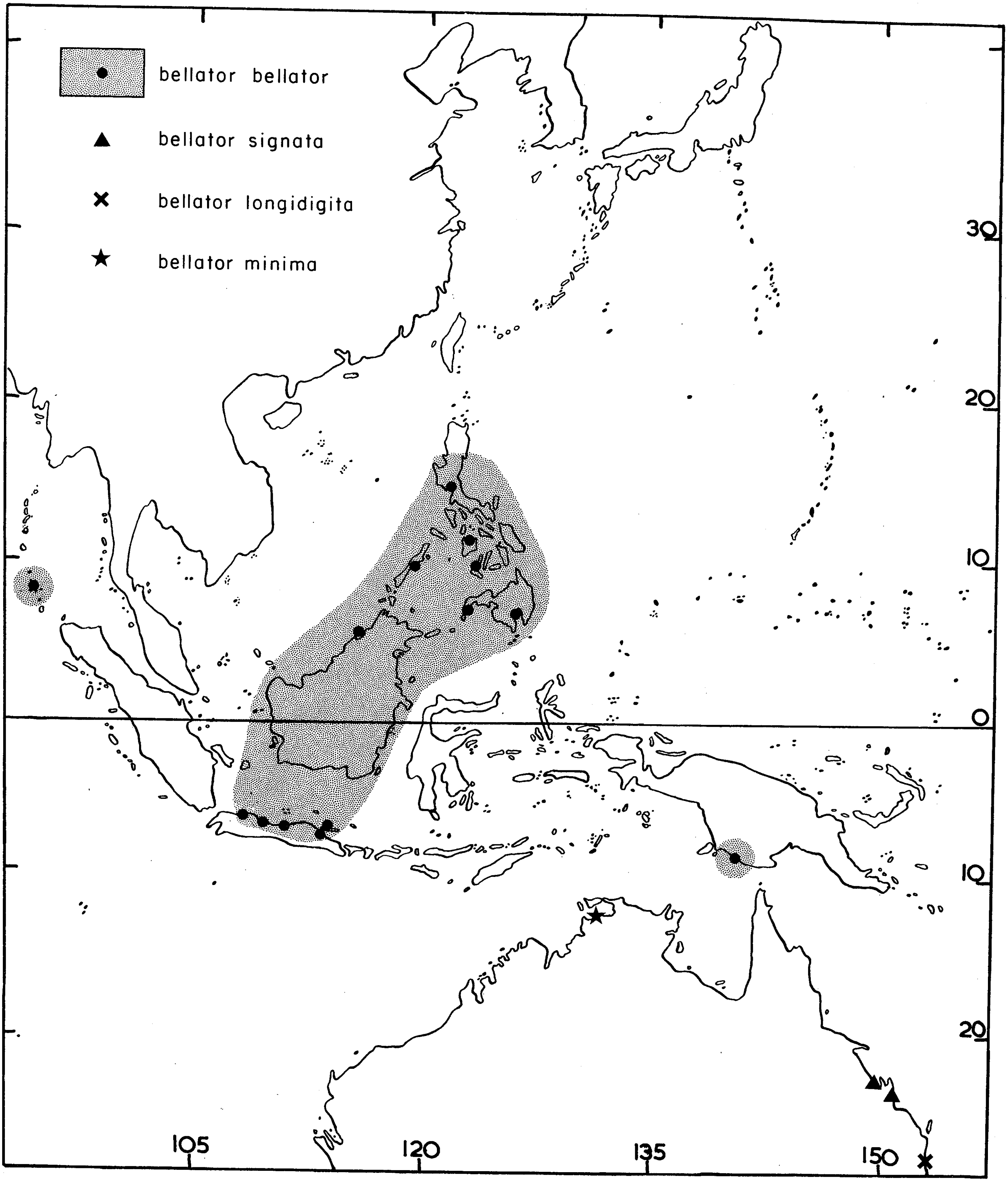
Species Name	Number of Map	Species Name	Number of Map	Species Name	Number of Map	Species Name	Number of Map
acuta	2	*festae*	16	*mordax*	12	*stenodactylus*	16
arcuata	19	*forcipata*	19	*musica*	17	*stylifera*	10
argillicola	15	*formosensis*	4	*oerstedi*	15	*subcylindrica*	11
batuenta	15	*galapagensis*	14	*ornata*	10	*tallanica*	15
beebei	16	*helleri*	15	*panamensis*	12	*tangeri*	8
bellator	3	*heteropleura*	10	*polita*	4	*tenuipedis*	15
brevifrons	13	*inaequalis*	15	*princeps*	9	*tetragonon*	4
burgersi	12	*inversa*	7	*pugilator*	16	*thayeri*	11
chlorophthalmus	5, 6	*lactea*	21	*pugnax*	10, 14	*tomentosa*	15
coarctata	19	*latimanus*	17	*pygmaea*	11	*triangularis*	7
crenulata	15	*leptochela*	15	*rapax*	14	*uruguayensis*	15
cumulanta	15	*leptodactyla*	17	*rosea*	2	*urvillei*	19
deichmanni	17	*limicola*	17	*saltitanta*	15	*vocans*	20
demani	2	*major*	10	*seismella*	4	*vocator*	13
dorotheae	15	*maracoani*	9	*speciosa*	15	*zacae*	14
dussumieri	18	*minax*	12				



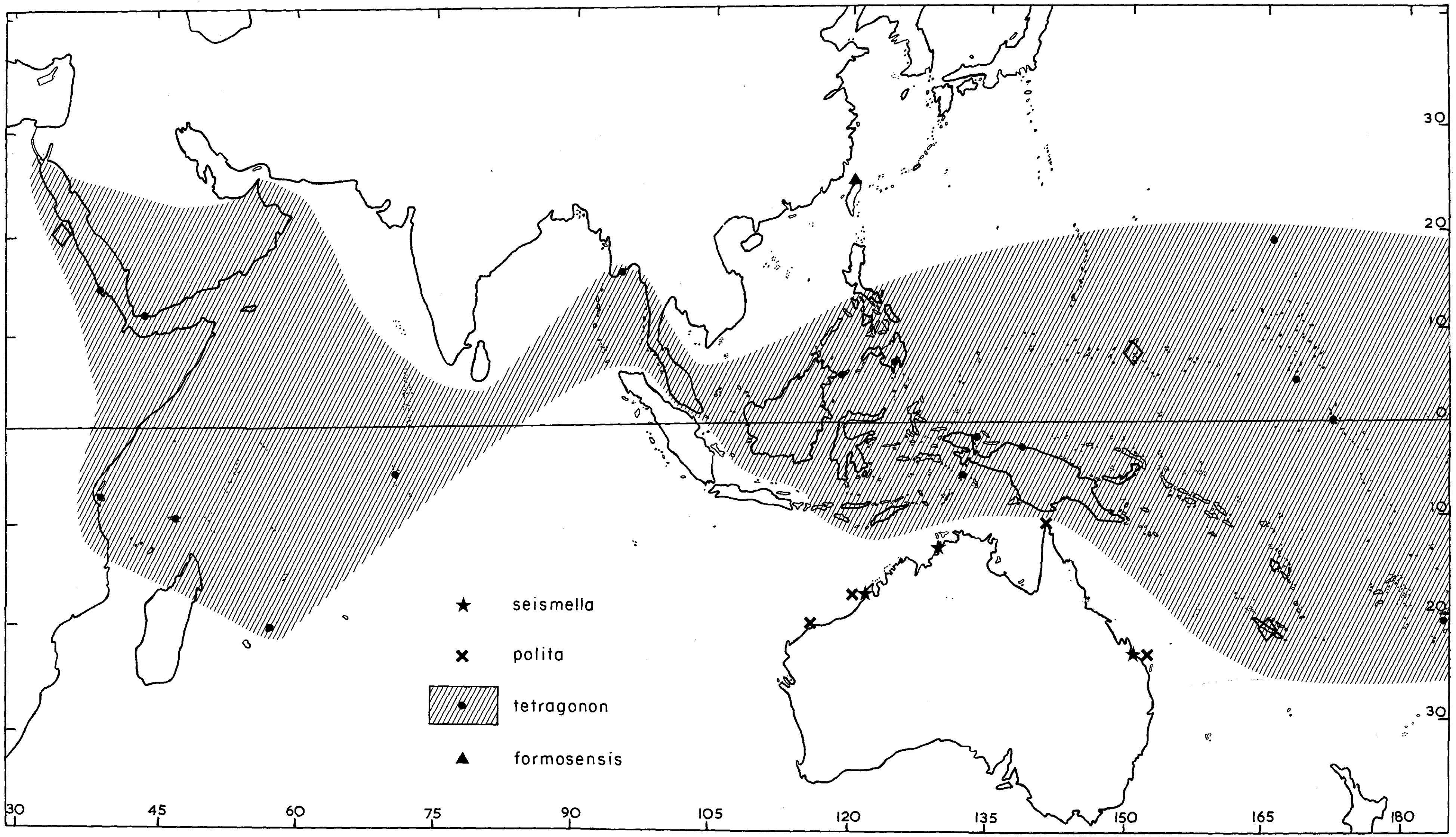
MAP 1. Distribution of the genus *Uca*, showing relative concentrations of species in different parts of the range. See p. 409ff.



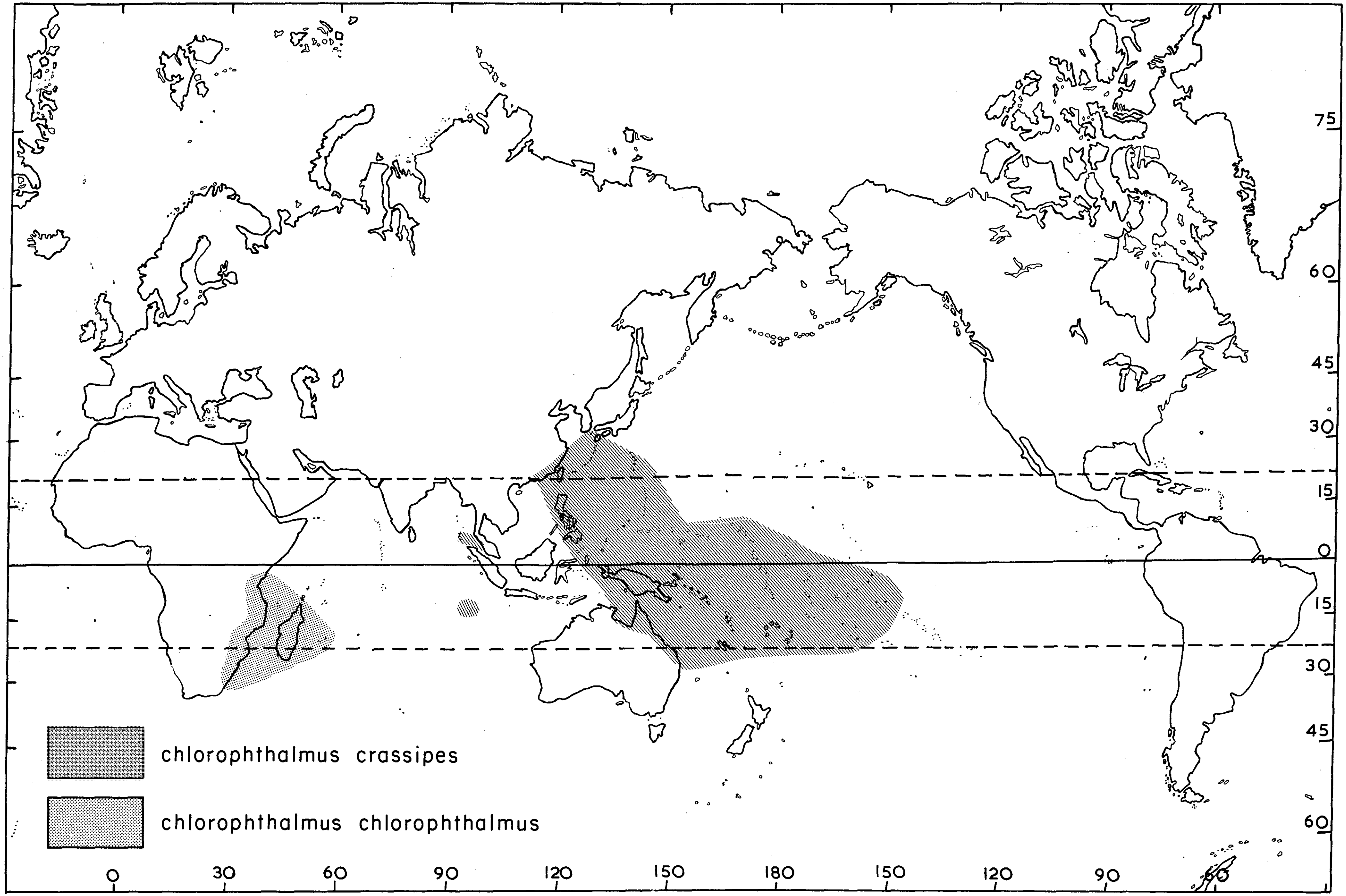
MAP 2. Distribution of the subgenus *Deltuca* (part). (General explanation: p. 409.)



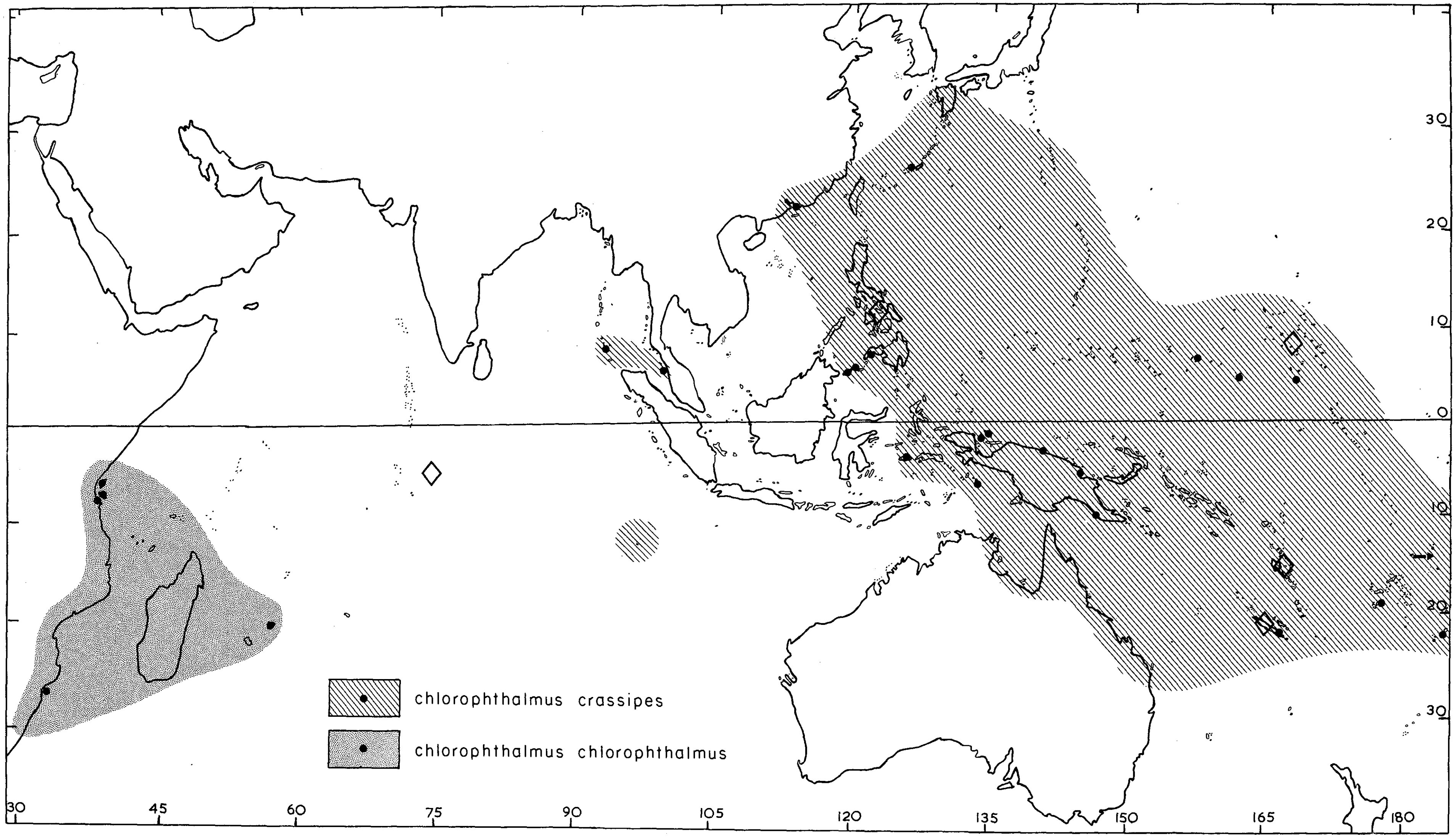
MAP 3. Distribution of the subgenus *Australuca* (part).
(General explanation: p. 409.)



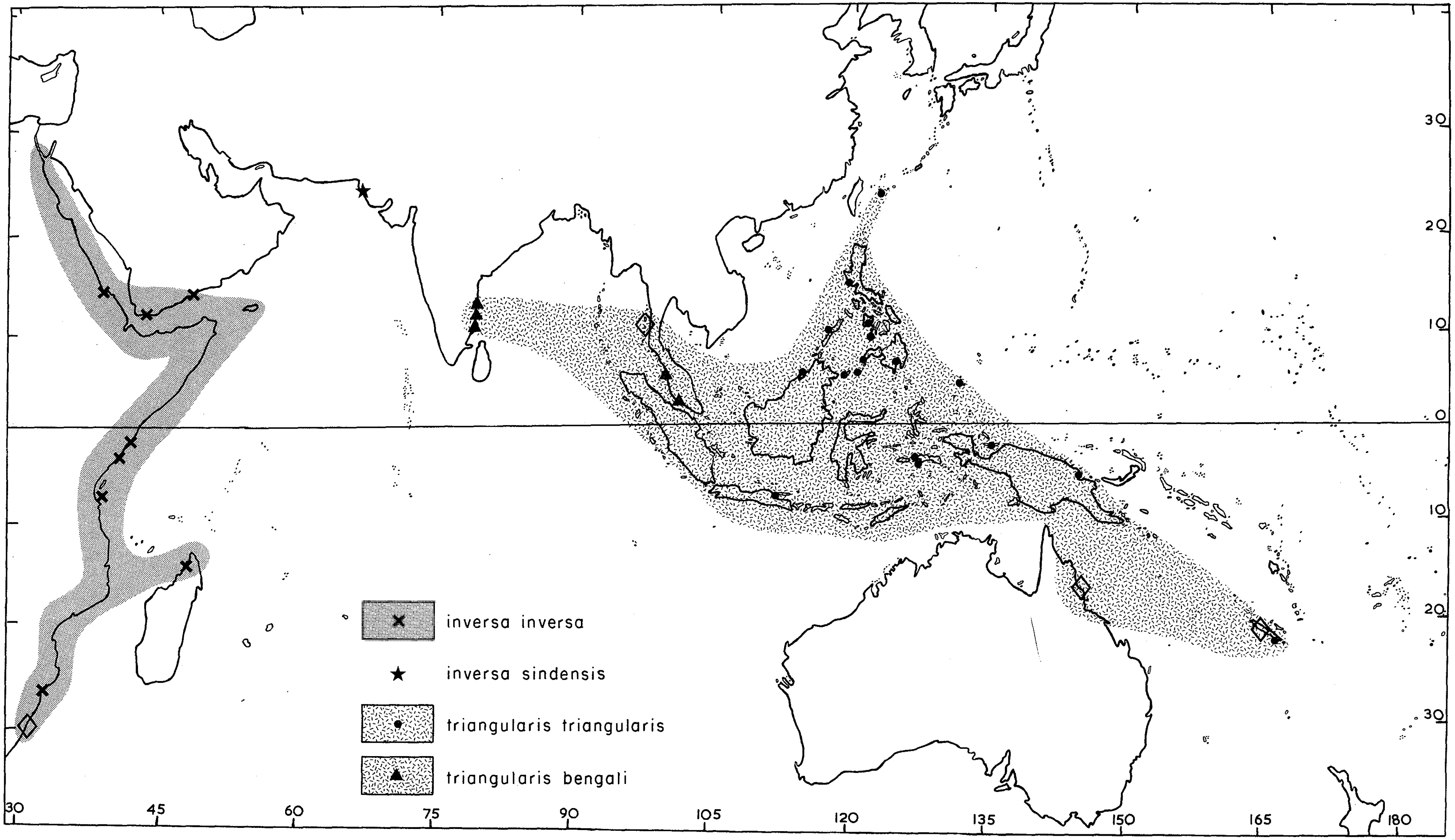
MAP 4. Distribution of the subgenera *Australuca* (concluded) and *Thalassuca* (part). (General explanation: p. 409.)



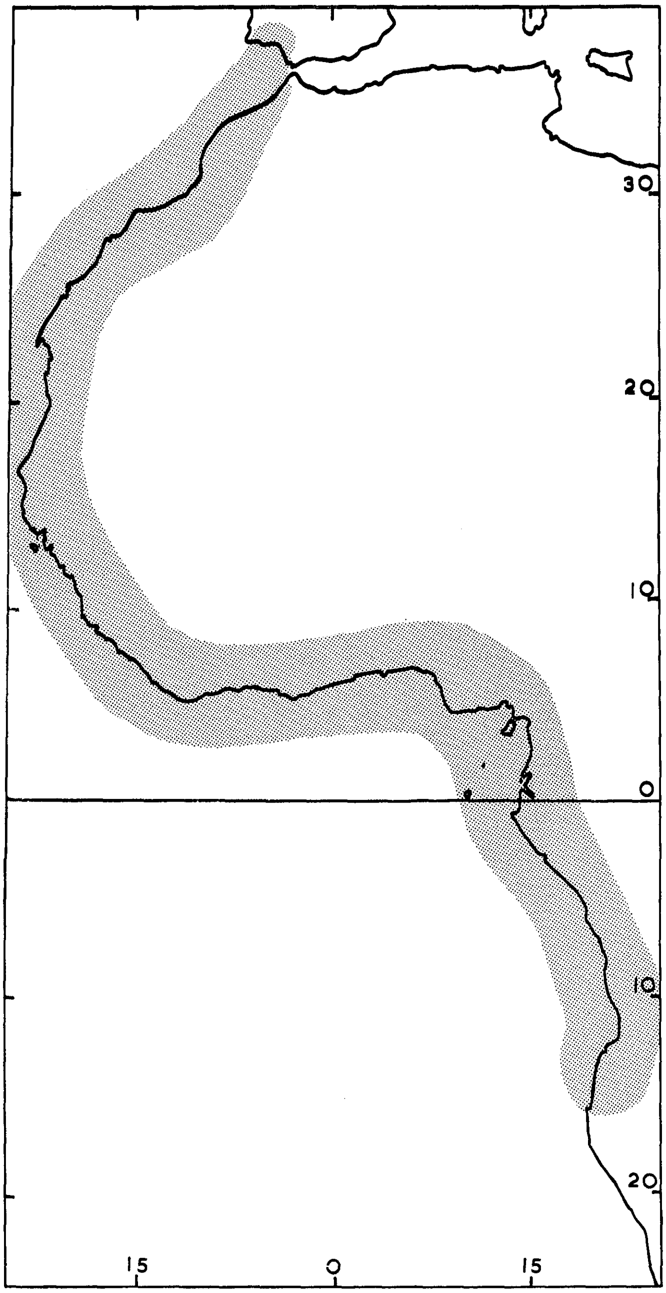
MAP 5. Distribution of the subgenus *Amphiuca* (part); see also Map 6. No definite record exists of the occurrence of *chlorophthalmus* in Australia. (General explanation: p. 409.)



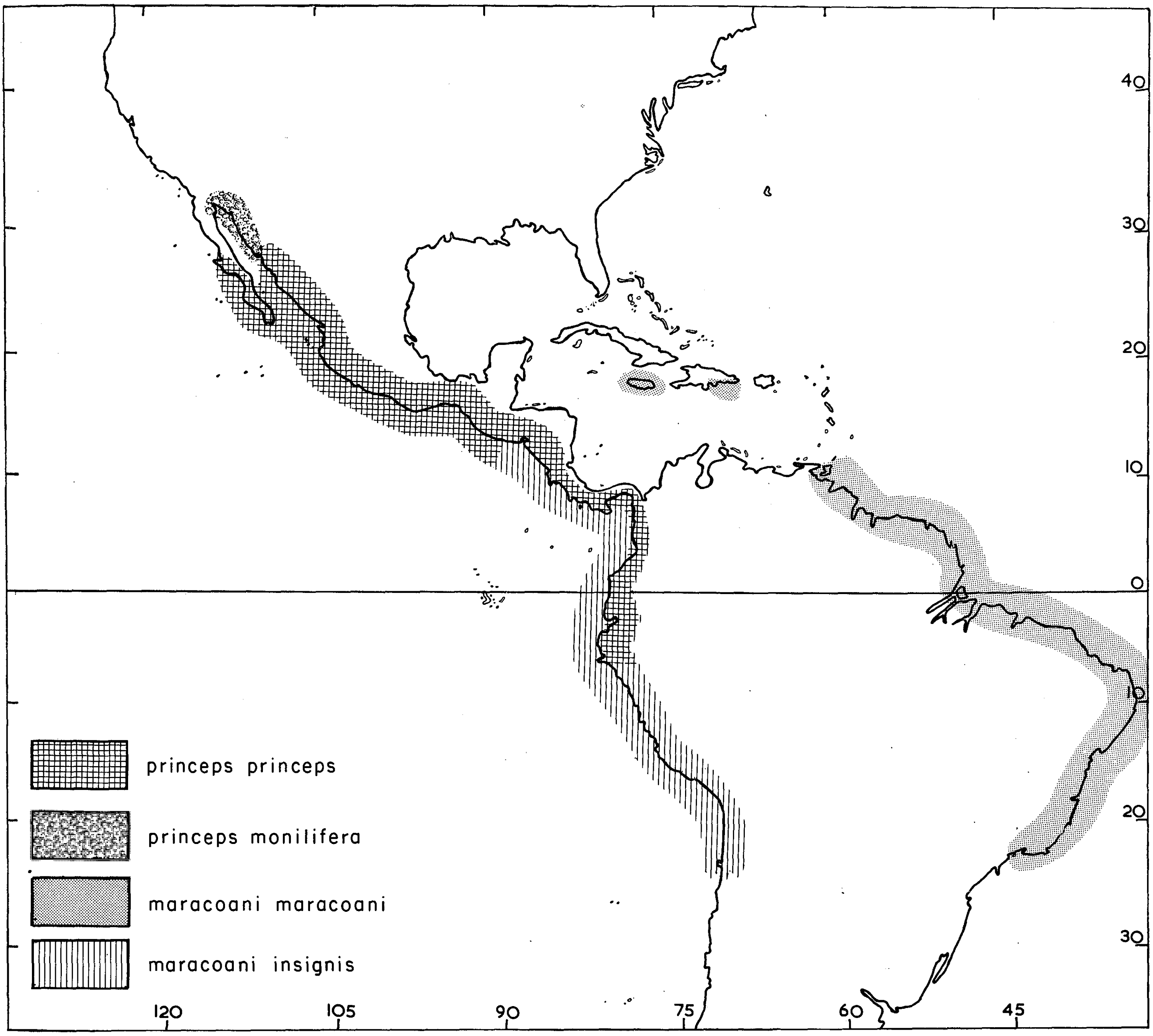
MAP 6. Distribution of the subgenus *Amphiuca* (part); see also Map 5. No definite record exists of the occurrence of *chlorophthalmus* in Australia. (General explanation: p. 409.)



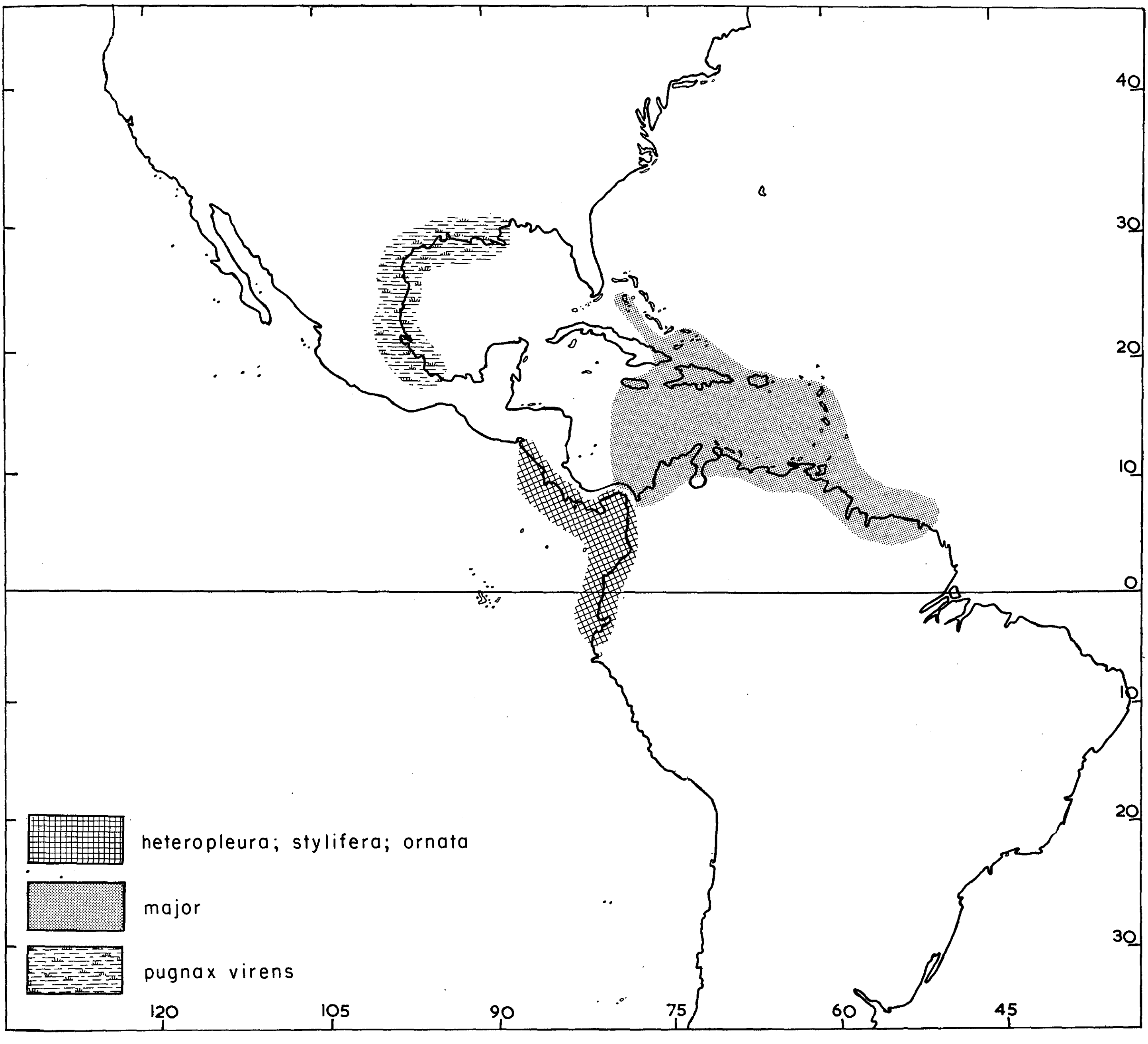
MAP 7. Distribution of the subgenera *Amphiuca* (concluded) and *Celuca* (part). Only one screen is used showing the distribution of (*Celuca*) *triangularis* because the normal boundaries between subspecies, particularly in Sumatra, are not yet known. (General explanation: p. 409.)



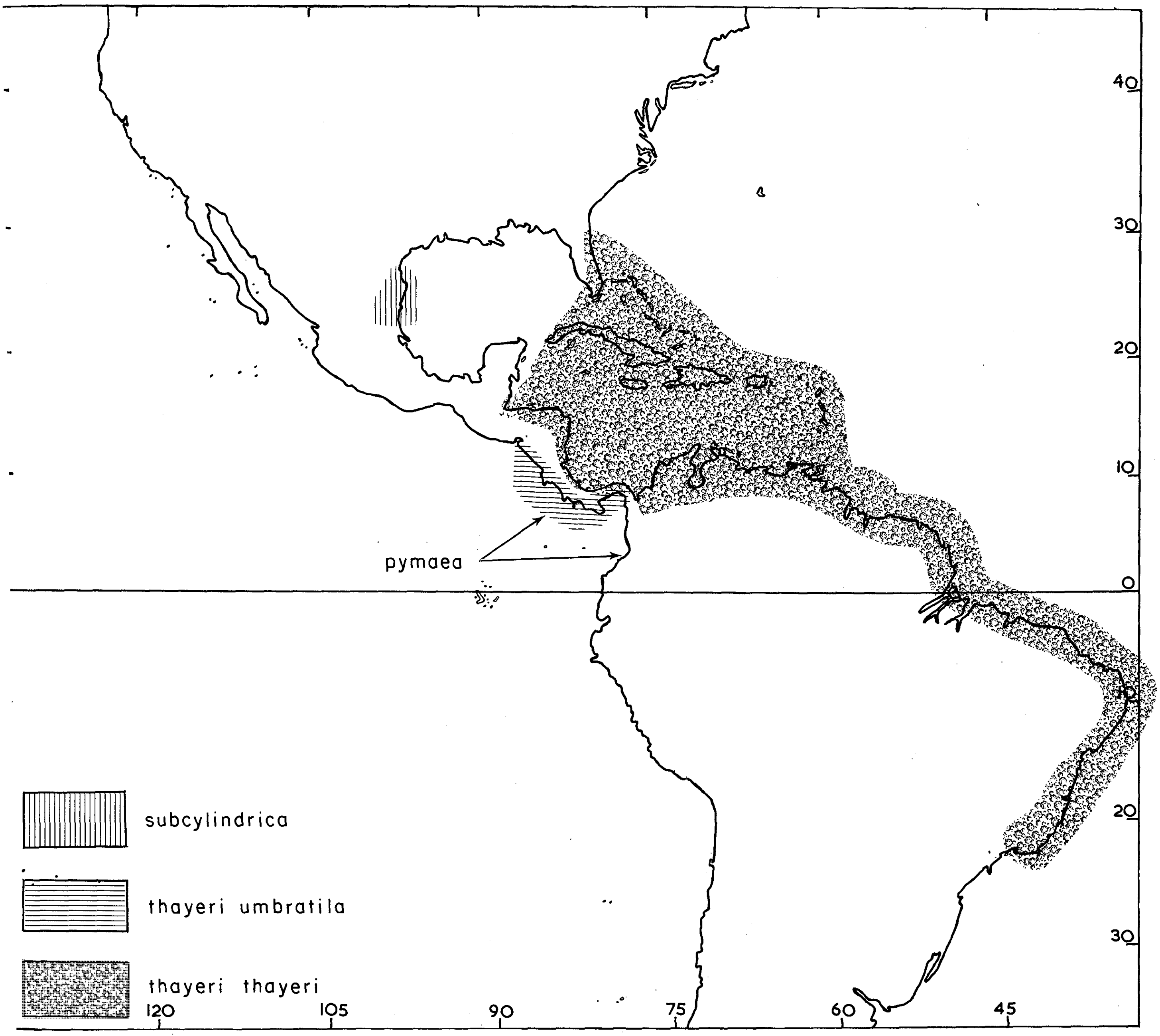
MAP 8. Distribution of the subgenus *Afruca* (complete), represented by the species *tangeri*. (General explanation: p. 409.)



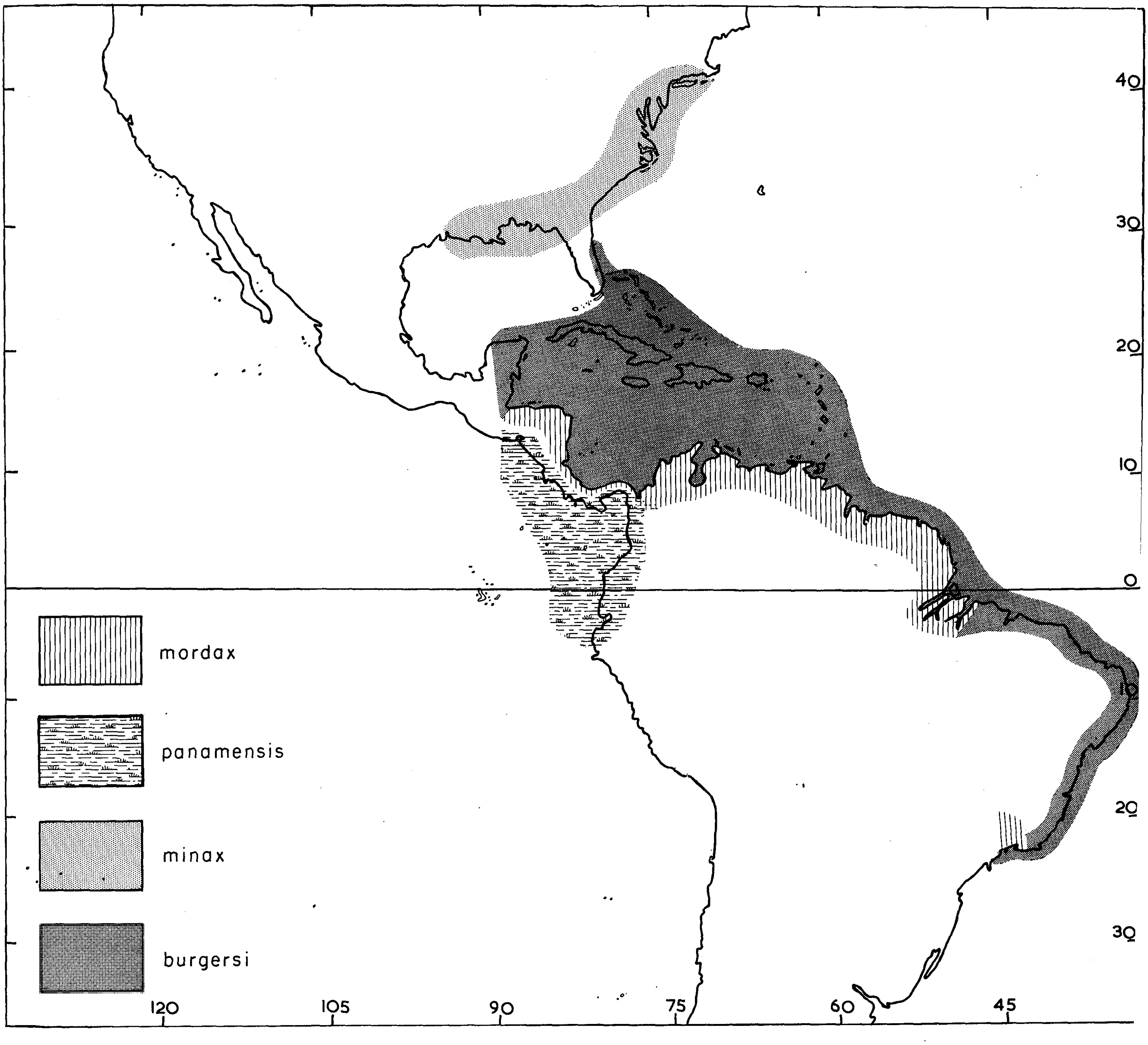
MAP 9. Distribution of the subgenus *Uca* (part). (General explanation: p. 409.)



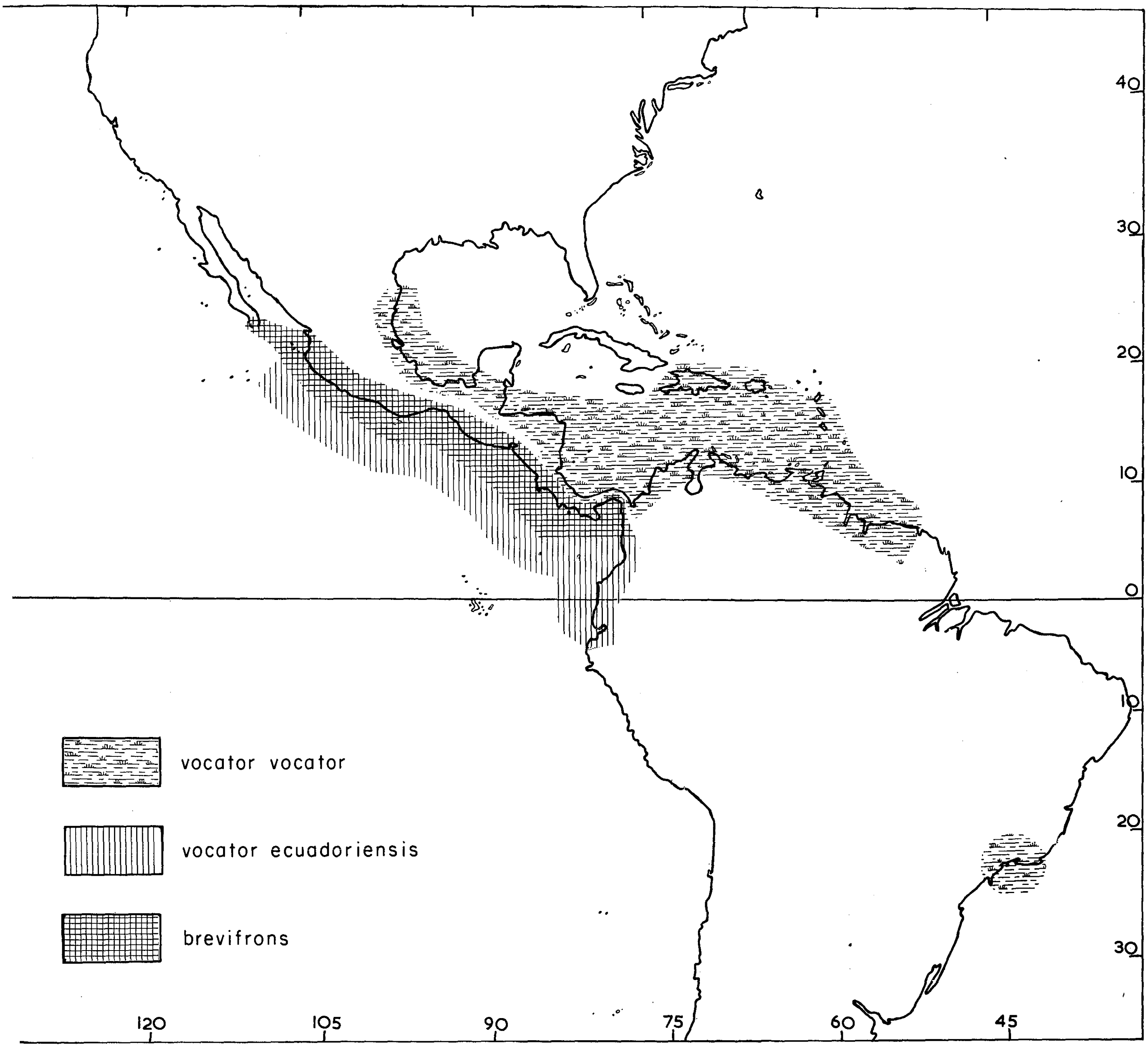
Map 10. Distribution of the subgenera *Uca* (concluded) and *Minuca* (part); for the distribution of (*Minuca*) *pugnax pugnax*, see Map 14. (General explanation: p. 409.)



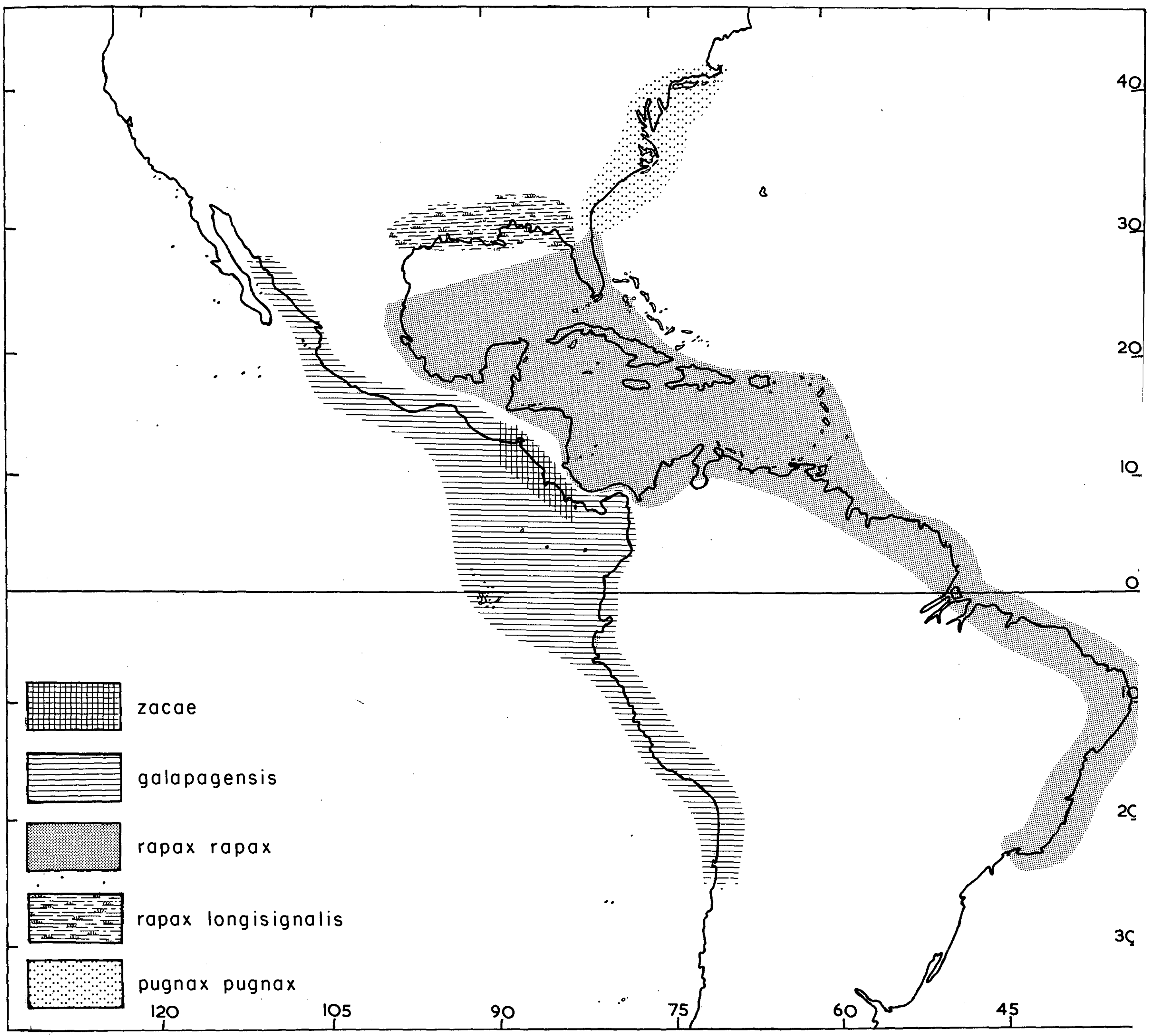
AP 11. Distribution of the subgenera *Minuca* (part) d *Boboruca* (complete). (General explanation: p. 9.)



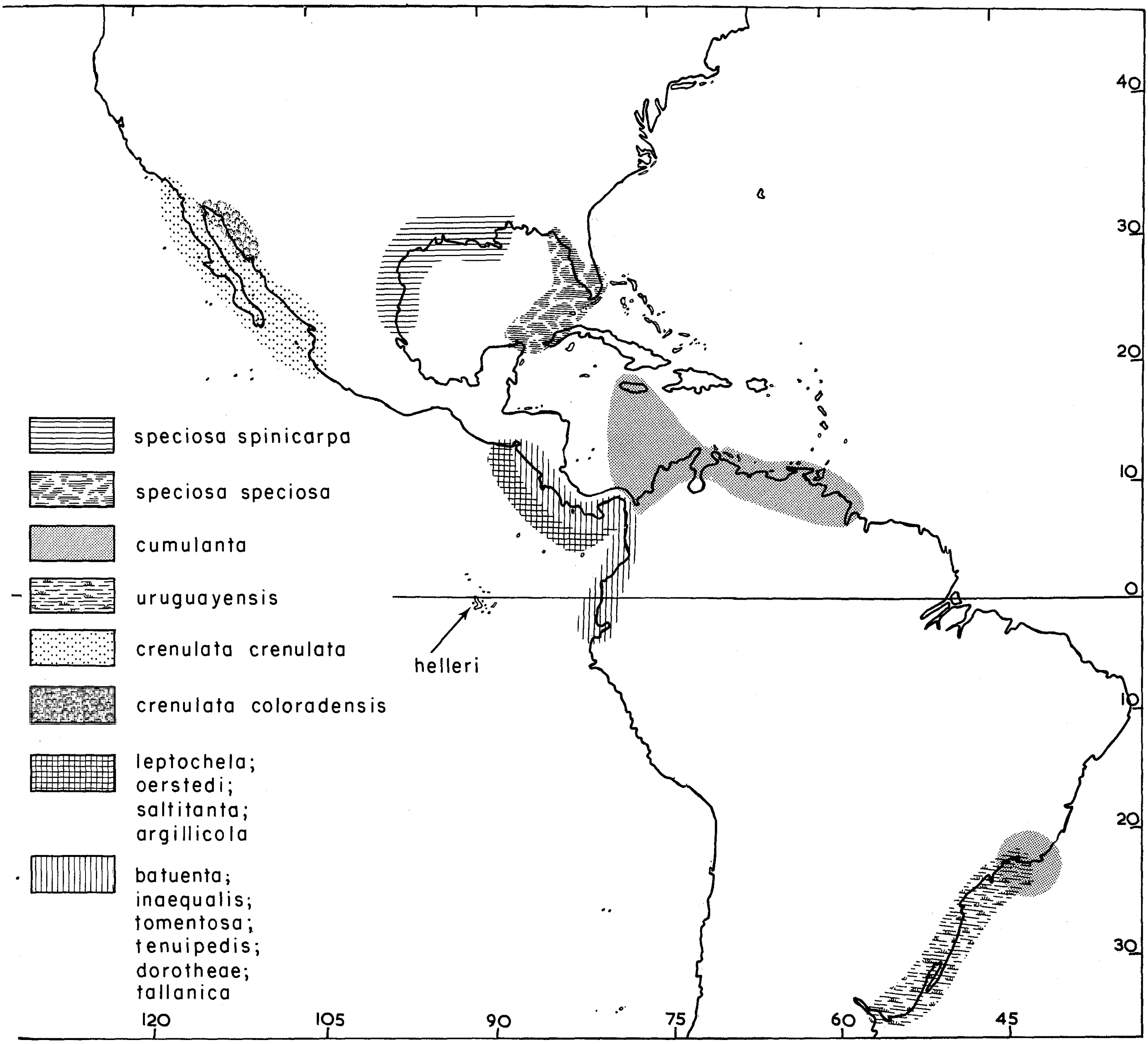
MAP 12. Distribution of the subgenus *Minuca* (part). (General explanation: p. 409.)



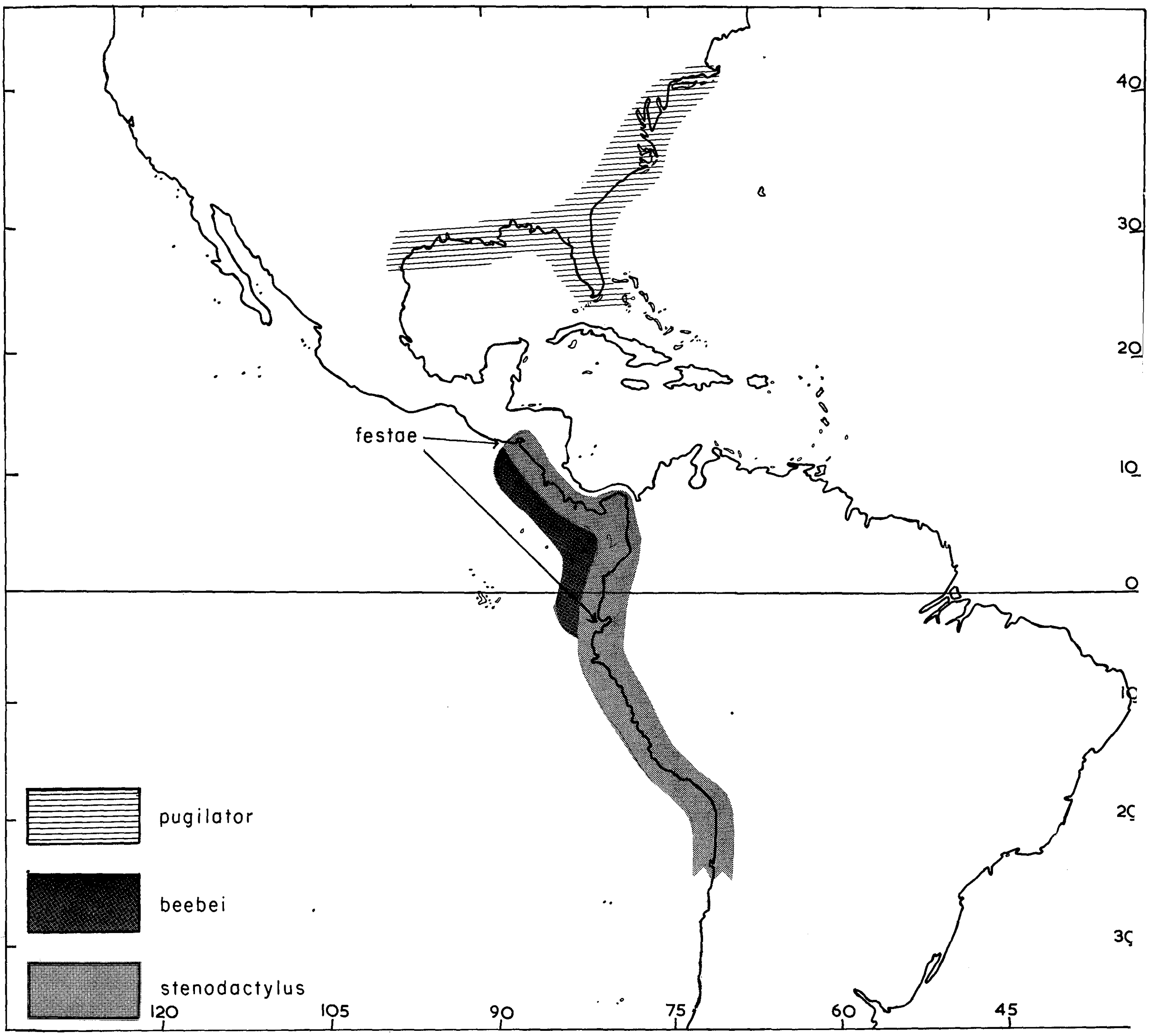
P 13. Distribution of the subgenus *Minuca* (part).
neral explanation: p. 409.)



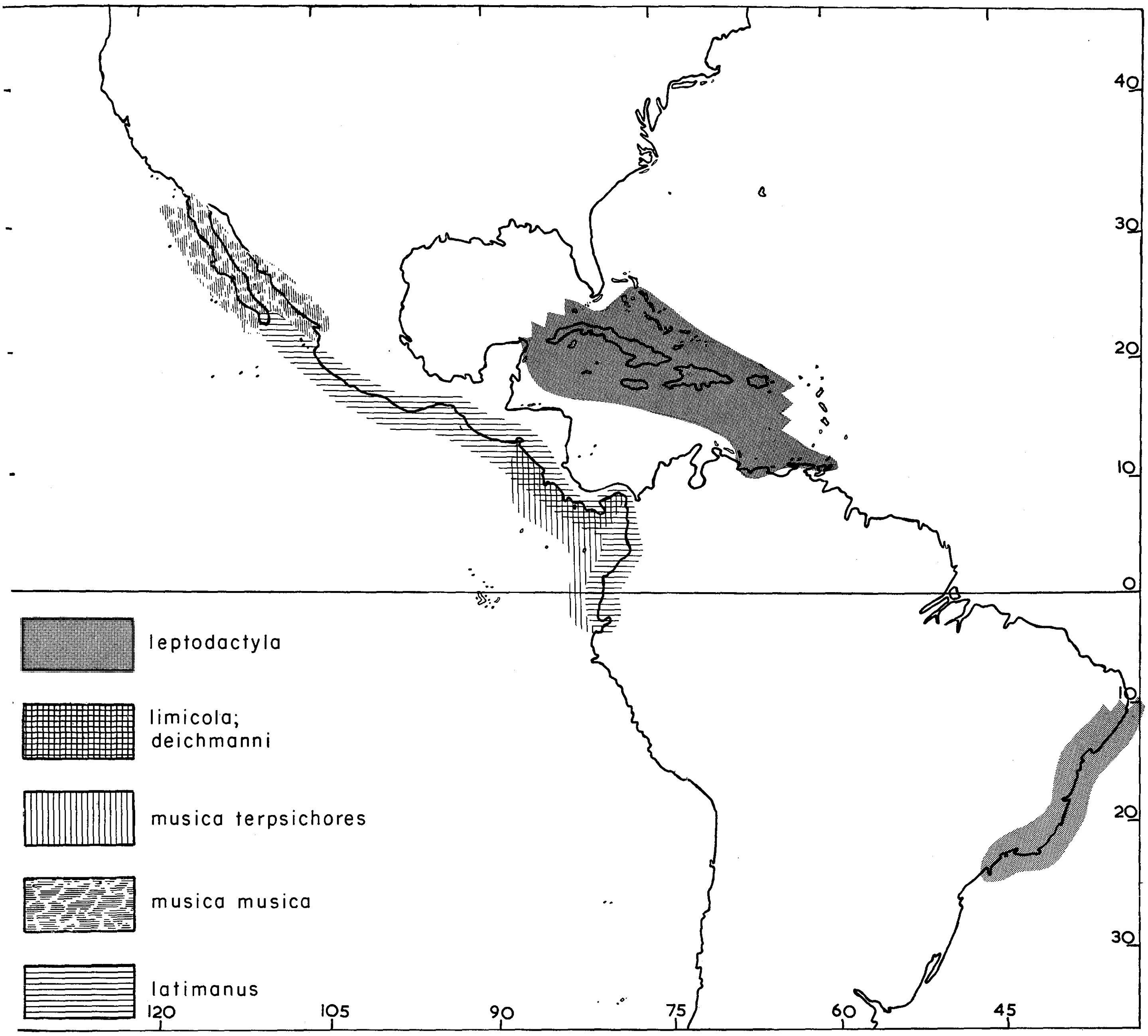
MAP 14. Distribution of the subgenus *Minuca* (concluded); for the distribution of (*Minuca*) *pugnax virens*, see Map 10. (General explanation: p. 409.)



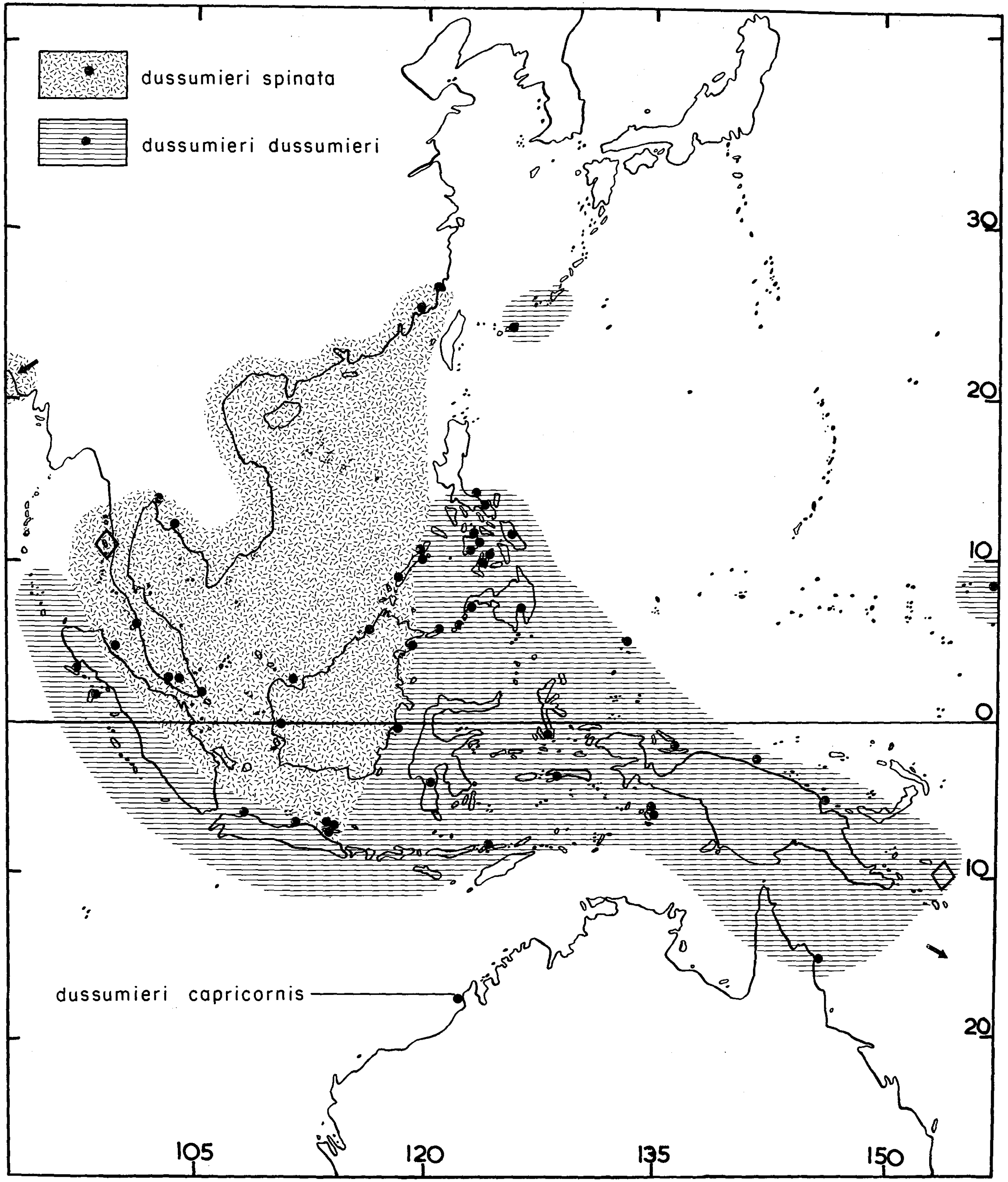
P 15. Distribution of the subgenus *Celuca* (part).
neral explanation: p. 409.)



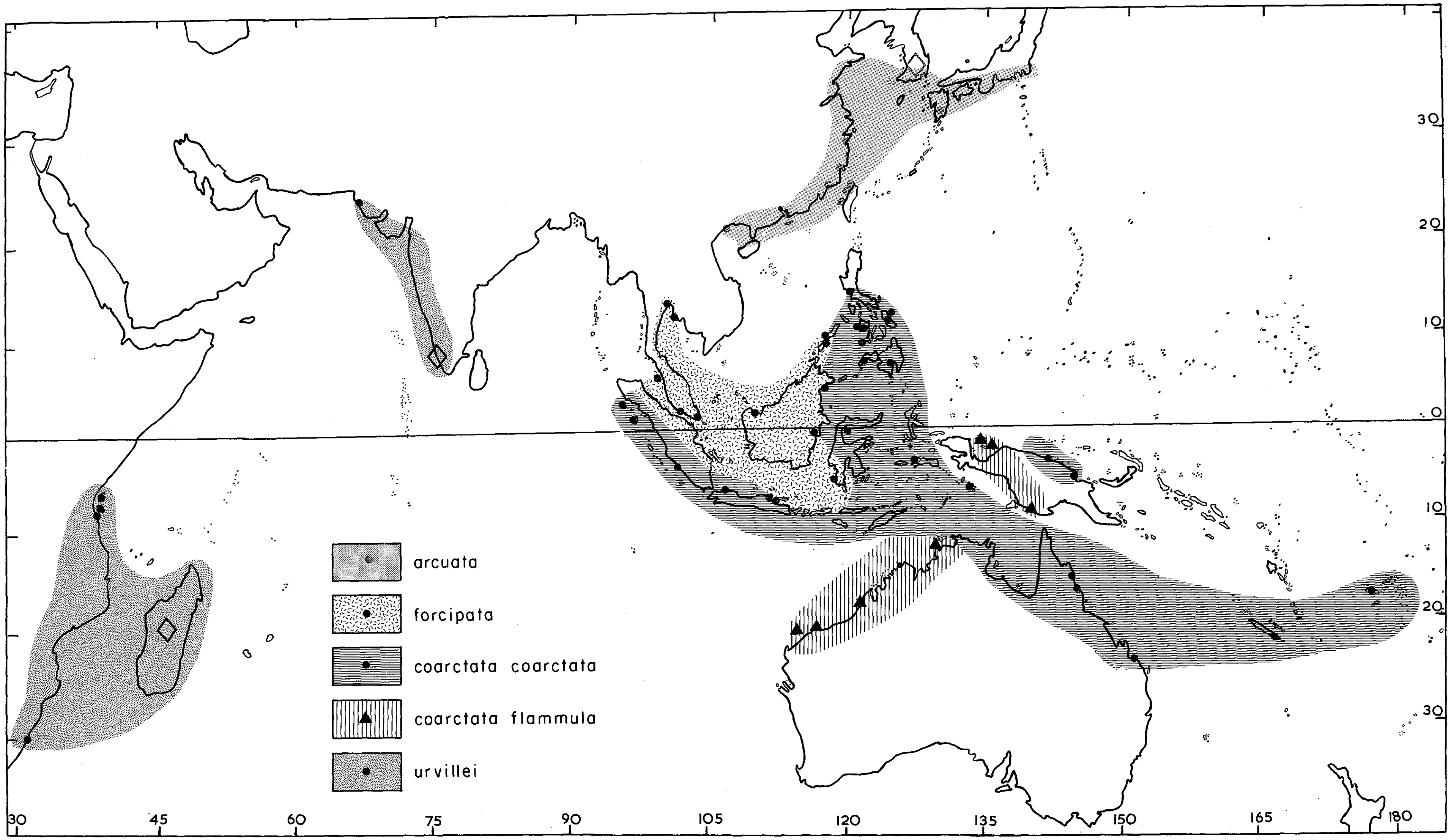
Map 16. Distribution of the subgenus *Celuca* (part). (General explanation: p. 409.)



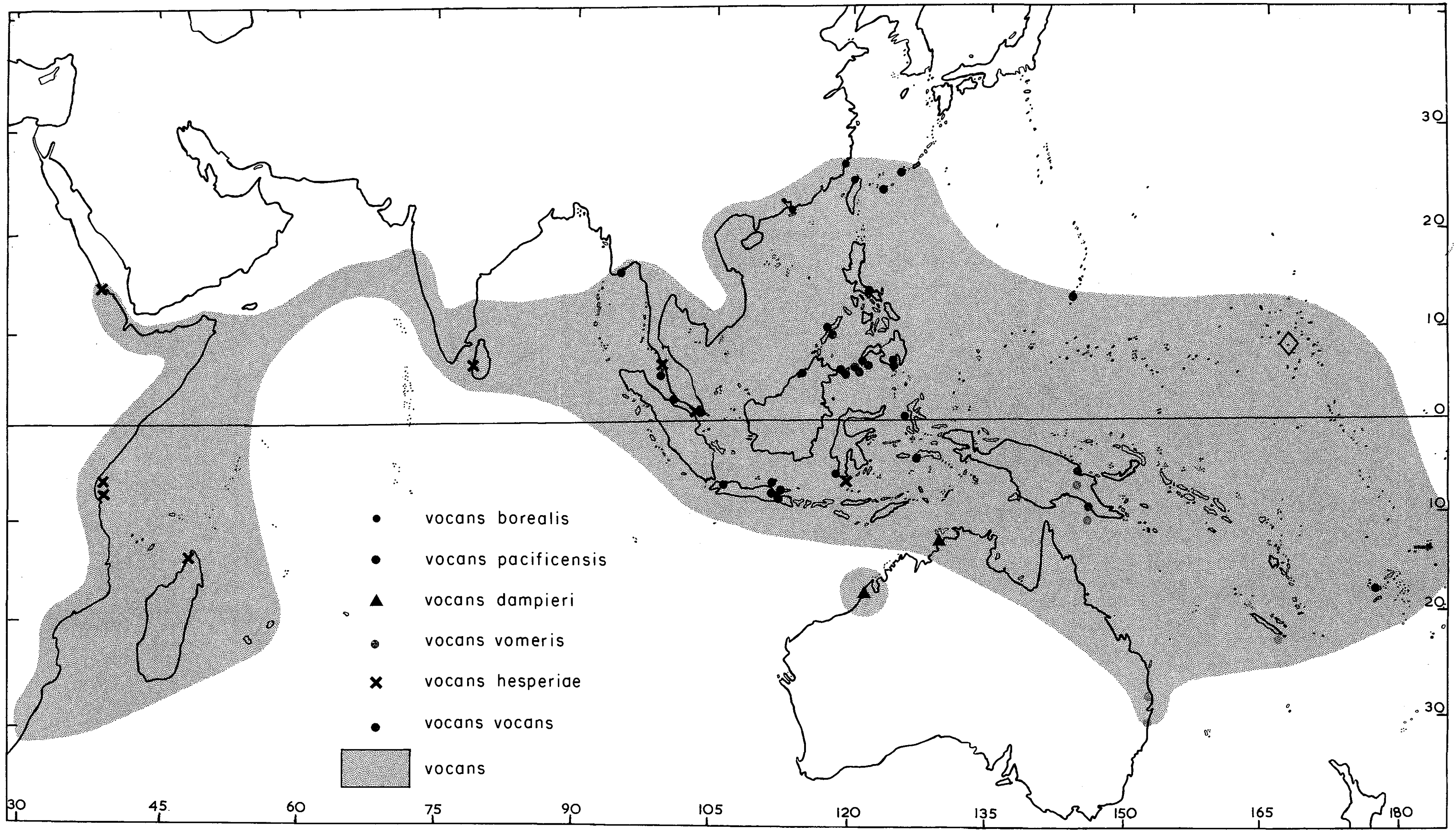
AP 17. Distribution of the subgenus *Celuca* (part).
eneral explanation: p. 409.)



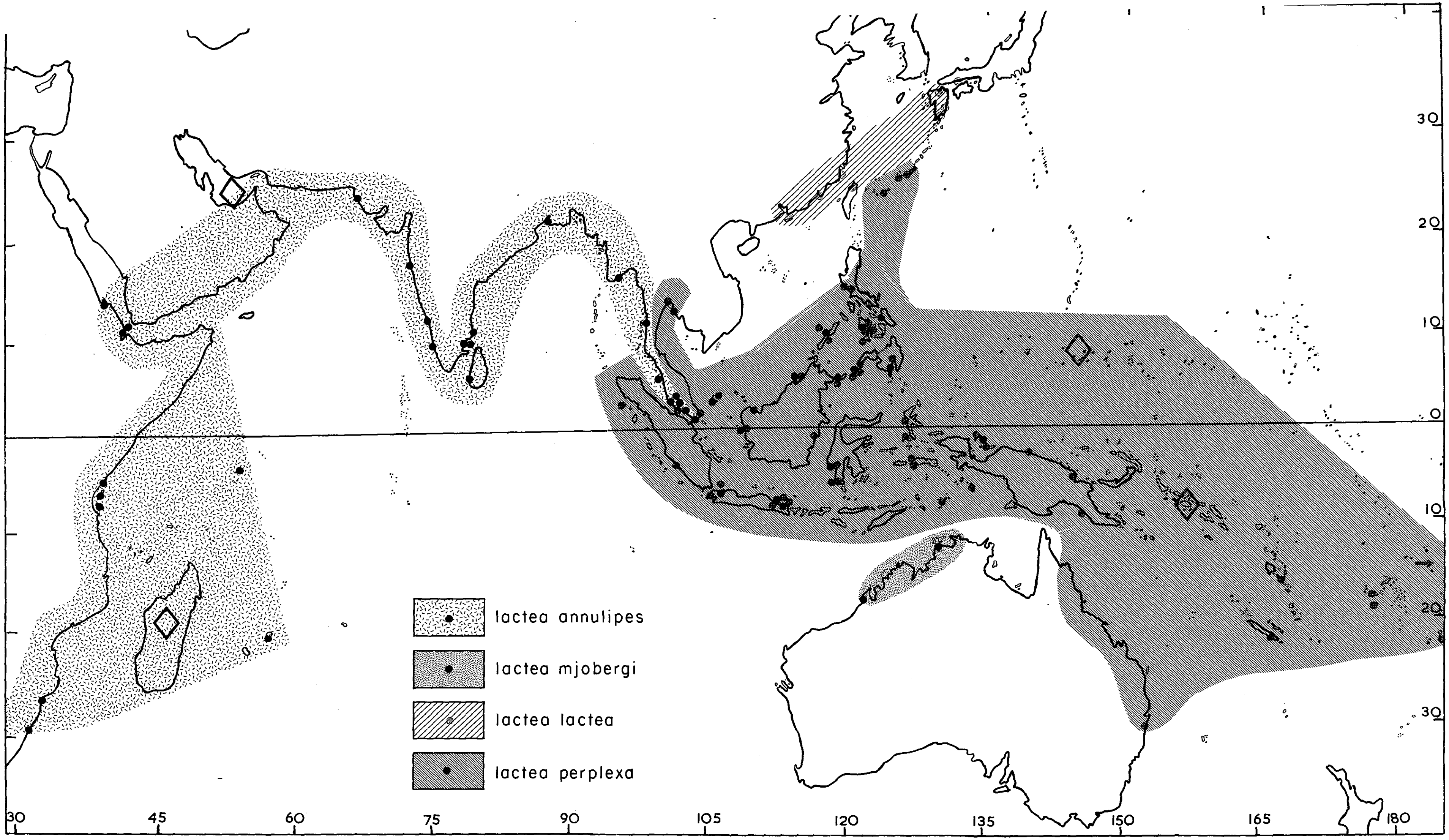
Map 18. Distribution of the subgenus *Deltuca* (part). *U. dussumieri capricornis* is also known farther south, from the Monte Bello Is., through a single young male (p. 592). The known range of *d. dussumieri* has recently been extended south to Moreton Bay, near Brisbane (p. 38). (General explanation: p. 409.)



MAP 19. Distribution of the subgenus *Deltuca* (concluded). The known range of *c. coarctata* in Australia has recently been extended south to Moreton Bay, near Brisbane (p. 57). (General explanation: p. 409.)



Map 20. Distribution of the subgenus *Thalassuca* (concluded). Only a single screen is used because of uncertain boundaries among the subspecies (p. 409). *U. vocans* has been reported once in recent years near Sydney (p. 94). (General explanation: p. 409.)



MAP 21. Distribution of the subgenus *Celuca* (concluded). (General explanation: p. 409.)

Part Two · Toward an Evolutionary Synthesis

Chapter 1. Zoogeography

OUTLINE

A. INTRODUCTION

Fiddler crabs, comprising the homogeneous genus *Uca*, are widely distributed throughout the tropics and subtropics of the world. Nine subgenera, totaling 62 species, are recognized in this contribution. More than two-fifths of these species are found only along the coast of the tropical eastern Pacific. Less than one-third occur in the entire Indo-Pacific region from East Africa to the Marquesas. On most coasts from one to three species extend into temperate regions.

The puzzles of the origins of *Uca* distribution yield both clues and permanent uncertainties in abundance. The clues, as usual, encourage hypotheses, while the uncertainties promptly reduce most reasoning to the level of speculation. The virtual lack of fossils remains a familiar obstacle.

The following survey first presents factual data on the modern distribution of the genus. A subsequent section considers the historical aspects of its zoogeography and presents several alternative explanations of the origins of the fauna; it is concluded that an Indo-Pacific center is most likely. The final sections in the chapter cover the distribution of the species among the subregions, with special reference to evolutionary aspects.

Contributions which, along with their references, will provide background material for the topics discussed include Durham (1950); Durham & Allison (1960); Ekman (1953); Garth (1960, 1965, 1966); Hedgpeth (1953, 1957.2); Hubbs (1960); Kummel (1961); Mayr (1963); MacGinitie (1958); Sverdrup, Johnson, & Fleming (1942); Trewartha (1954); Troll & Paffen (1963); Tweedie (1954); Umbgrove (1949). See also Hallam, ed. (1973).

B. SURVEY OF CURRENT DISTRIBUTION OF *Uca*

1. *Regional Distribution of Subgenera.* The distribution of the nine subgenera is shown in Table 7. It will be seen that four are confined to the Indo-Pacific,

three to the coasts of America, and one to the eastern Atlantic. The ninth, and largest, is primarily American, but has two representatives in the Indo-Pacific. Representatives of each of the subgenera found in America occur on both the Atlantic and Pacific sides of the Isthmus.

2. *Regional Distribution of Species.* The general distribution of the 62 species recognized in this contribution is shown in Map 1 and Tables 8 and 9. Eighteen occur in the Indo-Pacific, 43 on the coasts of America, and one in the eastern Atlantic. Fifteen of these American species are found in the Atlantic and 31 in the Pacific; the American total is limited to 46 because of the fact that three species are represented by forms so closely related on the two coasts that they are here considered subspecies, in spite of their current complete isolation by the Isthmus of Panama.

The richest area by far, with 30 species, is a small region of the tropical eastern Pacific, centering along the shores of the Gulf of Panama. Twenty-two of these 30 species are endemic (see below).

In the eastern Atlantic the genus is represented by one species, *tangeri*, that ranges the full length of the coast from the warm temperate climate of south Portugal to the subtropics of Angola. This species is related to American species of the subgenus *Uca*; it is, however, here given a subgenus of its own (*Afruca*). A member of the American subgenus *Minuca* perhaps occurs in West Africa (p. 327).

3. *Subregional Distribution of Species: Preliminary Survey.* The richest region of the Indo-Pacific is the area embracing the shores of northern Borneo, northern Sumatra, and the Bay of Bengal; here 11 species occur. Two other regions, the Philippines–East Indies Axis and northeastern Australia, are almost as rich, with 10 species each.

To the west, north, and east, numbers decrease, as follows: northwest Australia has eight species, East Africa–Western India, six; China–West Taiwan–Japan, seven; and the Pacific Islands, five.

On American coasts the following distribution prevails. From southern California to the southern border of Mexico, five species; from the Gulf of Fonseca to Peru, 30 species; from Chile, perhaps as many as three species. From the temperate eastern United States (excluding northeast Florida), three species; from the Gulf states, six; subtropical Florida, five or six; tropical western Atlantic, from Mexico and the Caribbean to Rio de Janeiro, Brazil, 12; southern Brazil, five or six; Uruguay and Argentina, one.

These subregional distributions will be considered in more detail, in relation to the evolution of the species, in the sections starting on p. 435.

4. *Allopatric Distribution in the Indo-Pacific Region.* Among the 18 Indo-Pacific species, one (*tetragonon*) ranges, without regional variations making useful the erection of subspecies, throughout the tropics from the Red Sea to the Tuamotus. Three species, divided here into two to six subspecies each, show an almost equally wide range (*vocans*, *chlorophthalmus*, *lactea*). Four species, each comprising two to four subspecies, have ranges roughly confined to the area bounded by eastern India, the Philippines, and the tropical coasts of Australia (*dussumieri*, *demani*, *bellator*, *triangularis*); a partial exception, *dussumieri*, alone occurs north of the tropics in China and the Nansei (Ryukyu) Islands.

Two groups of species are regarded as superspecies (*acuta* and *coarctata*). One of them, *coarctata*, is composed of four species and ranges throughout the Indo-Pacific. The second, *acuta*, is found from Fukien in northern China to Indonesia and from the Ganges delta to Java; it includes two species of which one subspeciates.

5. *Allopatric Distribution in the American Region.* All of the 12 species in the tropical western Atlantic have close relations across the Isthmus of Panama. In three of them, *maracoani*, *thayeri*, and *vocator*, the allopatric representatives are here given only subspecific rank. A fourth, *rapax*, is morphologically so close to *galapagensis* that the specific standing accorded them may be illogical (p. 183). The remaining eight species in the western Atlantic appear sufficiently distinct from their Pacific counterparts to be counted without hesitation as full species.

Along both the Pacific and Atlantic coasts the erection of subspecies occasionally appears both justified and desirable. So far there is little or no evidence of the formation of clines; adequate meristic data, however, remain virtually absent.

6. *Endemism.* In the entire Indo-Pacific region only three species have narrow ranges. *U. polita* and *seismella*, both in the subgenus *Australuca*, are confined to Australia. *U.* (*Amphiuca*) *inversa* is known only in eastern Africa and in Pakistan, at Karachi, with a distinct subspecies in each of the two areas.

The contrast with the situation in America is striking. It has already been mentioned that 22 species are confined to a small tropical area on the Pacific coast of America. This strip extends only from about lat. 14° N. to about lat. 3°30′ S., or a straight distance of about 1,100 miles. The region includes part of the Pacific coast of El Salvador, and extends to the extreme northern edge of Peru, on the southern margin of the Gulf of Guayaquil.

Endemism is also apparent near the latitudinal extremes of the genus on three of the four American coasts. One species is endemic on the west coast of California and in northwest Mexico (*crenulata*); northern subspecies of two others (*m. musica* and *princeps monilifera*) are virtually confined to the

Gulf of California; two endemic species are found on the south and east coasts of the United States (*minax*, *pugilator*); one occurs only from subtropical Brazil to Buenos Aires, Argentina (*uruguayensis*).

In the Indo-Pacific, on the contrary, the few species ranging into temperate climates are, with two exceptions, merely widespread species from the tropics. The exceptions are *arcuata* and *formosensis*. Three other species extending into Indo-Pacific areas of winter chill are represented by subspecies of narrow range (*acuta*, *vocans*, *lactea*). Finally, a tropical subspecies of *dussumieri* ranges without obvious morphological changes north to near Fu-chou.

The present extremes of distribution in the genus are summarized in Table 7.

7. *Summary of Current Distribution of Species.* By far the richest area in number of species is the west coast of tropical America (eastern Pacific), with 30 species. The tropical American east coast (western Atlantic), the Indo-Malayan region (tropical west Pacific) and the northeast Australian (Solanderian) region are comparable to one another, having 10 to 12 species, one-third to two-fifths of the number found in the tropical East Pacific. Only six species occur in eastern Africa, while the fauna is poorest near the northern and southern limits of the genus range (one to two species), the eastern boundary of the Indo-Pacific (two) and, especially, the eastern Atlantic (one or, possibly, two).

C. HISTORICAL ZOOGEOGRAPHY

The question of the genus origin may now be discussed. Later the background of speciation in the geographical subregions will be considered.

Among the references listed on p. 431, those of the most direct aid in preparing this section have been Durham (1950), Ekman (1953), Kummel (1960), MacGinitie (1958) and, for recent views on several dates, Hallam, ed. (1973).

1. *Factors Concerned in Postulating the Geographical Origin of* UCA. As in all such questions, five major lines of evidence must be examined: first, the geological and climatic history of the world; second, the present distribution of the group; third, its fossil history; fourth, evidence from the group's systematics, especially from comparative morphology and social behavior; fifth, the group's ecological requirements. Although the present discussion is concerned primarily with the first two, the other aspects, discussed in more detail elsewhere, will be mentioned from time to time.

As mentioned in the beginning of this chapter, the fossil record is almost nonexistent. Only three specimens referrable to *Uca* appear to exist, two from Pliocene beds, one from Pleistocene, and all in America; all are similar to contemporary American species (pp. 127, 157). A fourth fossil, attributed by Desmarest (1822) to the genus *Gelasimus* (= *Uca*) has disappeared (p. 324). In addition, an ocypodid from the Pliocene of Jamaica resembles *Macrophthalmus*, an Indo-Pacific genus (Rathbun, 1919).

Three major areas seem to be possible centers of early *Uca* evolution and dispersal. The genus may have evolved in the circumtropical area during the greatest expansion of the Sea of Tethys, or, somewhat later, in either tropical America or in the Eastern Pacific. A temperate or polar origin seems unlikely because of the warm-climate distribution of almost the entire highly various family. In the present section each of these major possibilities is considered in turn.

The following annotated list assembles a number of geological, climatic and ecological factors which were probably, as in the evolution of so many other marine animals, of primary importance in the history of the group. This attempt to understand *Uca*'s particular characteristics requires their review in juxtaposition, in spite of the familiar nature of some of the material.

1. A warm global climate existed from the Cretaceous through the Eocene, with the tropics extending far north along the Pacific and Atlantic coasts.
2. The climate gradually cooled from the Oligocene through the Pleistocene.
3. During these periods the Atlantic Ocean cooled drastically. This was particularly true of the eastern Atlantic, in contrast to the eastern Pacific and Indo-Pacific regions where cooling was, respectively, slight and absent. There was a consequent striking impoverishment of Atlantic fauna, which has been demonstrated in many groups of animals. In other marine and littoral groups, however, including echinoderms and certain crabs, the Caribbean is now richer in species than is the tropical eastern Pacific.
4. The vast Tethyan seaway gave access at its maximum extent from the eastern Pacific all the way eastward to China. After the beginning of the Oligocene it dwindled, and from the Miocene onward it was impassable as a route between the Atlantic and Indian Oceans.
5. The last possible exchange of marine faunas between the tropical Atlantic and Pacific took place near the end of the Pliocene, perhaps 5,000,000 years ago, ceasing when, about that time, the Isthmus of Panama became completely emergent.
6. The major islands of the Philippines and East Indies, at present so rich in species in many groups

of animals, were apparently rarely above water before the Eocene.

7. The Sunda Shelf was emergent for much of the period from the Pliocene to the end of the Pleistocene. This area extended the coast of southeast Asia to include Borneo, Java, Sumatra, and many lesser islands, acting as an effective barrier between the China Sea and Philippines area on one hand and the Bay of Bengal and western regions on the other. After the Pleistocene, seas covered this shelf region, the East Indies assumed much of their present form, and free dispersal of organisms once more was possible between the Indian Ocean and the north tropical Pacific. This submersion of the Sunda Shelf probably took place not more than 10,000 years ago.

8. A similar barrier, the Sahuli Shelf, probably connected northern Australia and New Guinea from time to time over long periods, separating the littoral fauna of western and eastern Australia. It seems likely that the last submersion of that barrier also occurred soon after the Pleistocene's end.

9. Intense orogenic activity took place in the Philippines–East Indies area from the Pliocene onward.

10. In contrast, the shores of the Indian Ocean, both east and west, were then quiet.

11. The East Pacific Barrier is as potent a force in this group of animals as in practically all other groups. There is no evidence that any modern Indo-Pacific species of *Uca* has ever reached America or vice versa, much less become established there. Nevertheless, two considerations make caution in this area of importance. First, the timing of metamorphosis of some pelagic larvae into littoral crustaceans is partly controlled by characteristics of the water, the molts to post-pelagic stages apparently being triggered by chemical factors occurring near land (Garth, 1966, and refs.). Second, the Indo-Pacific ocypodid, *Ocypode ceratophthalmus*, occurs on Clipperton Island along with 15 other species of brachyuran crabs that are of Indo-Pacific origin and only 18 others that are American (Garth, 1965). The distance from Clipperton to the nearest point on the Mexican coast is about 600 nautical miles.

12. The mid-Atlantic, at least in the period from the late Tertiary to the present, has been an almost equally potent barrier.

13. *Uca* is essentially a tropical genus, always reaching its greatest development within the true tropics. A few species, however, have adapted to freezing winter temperatures, hibernating for months at a time. The genus is absent from cold temperate and boreal climates.

14. As in other groups of littoral animals, regions with high tides support higher numbers of species, other factors being equal.

2. UCA *as a Possible Member of the Old Mesozoic Circumtropical Fauna.* According to this view, *Uca* would have formed part of the fauna evolving on the shores of the Tethys, when the vast sea reached its greatest extent. At this time, between the late Mesozoic and the Eocene, no barriers of land or climate stood from the eastern Pacific eastward to China. If the genus evolved under these conditions, no Tethyan neighborhood is more likely than another to have been the center of *Uca* evolution. Similarly, no early differentiation of American and Indo-Pacific forms would be expected.

Ekman (1953) has been the strongest recent advocate of descent of circumtropical organisms from marine animals of this old warm water shelf. This view is certainly the correct explanation of the present-day distribution of a number of groups, notably corals, echinoderms, and some fishes. Ancestral forms no doubt circulated freely throughout the Tethyan realm and on across the Pacific where they were stopped—as today—by the East Pacific Barrier. Ekman does not discuss the possibility of migration of warm water shelf species across the Behring bridge in the days when temperatures were higher.

As listed briefly under points 3 to 5, p. 433, three great geological and climatic events broke up the circumtropical fauna, starting roughly in the Oligocene, culminating in the Pleistocene, and ending with that epoch's close.

First, the Tethys became reduced, resulting in the ultimate blocking off of the Atlantic from the Indian Ocean by emergent Asia Minor, Iran, and Suez. The last narrow passage closed sometime in the Miocene; the western end of the Mediterranean had also come to have such a narrow transit to the Atlantic that as a funnel for dispersal it had long been impractical.

Second, the last Central American passage between the Atlantic and Pacific was closed by land emerging near the end of the Pliocene, about five million years ago. Until then, via several seaways from Tehuantepec in the north to one across present-day Colombia in the south, passages of various widths had been freely open. During much of the time, wide seaways existed.

Third, the climate of the Atlantic deteriorated progressively from the Oligocene on. The eastern Atlantic was most affected. The West Indies were also chilled from time to time, although not so drastically; nevertheless, it was enough to kill off many formerly prominent elements of the fauna. A notable example is coral of the genus *Pocillopora*, which now remains abundant and ecologically important both in the eastern Pacific and from mid-Pacific to the Red Sea. At intervals only the South American shelf, the region of Amazonica, was left as a dubious refuge for creatures of tropical shores. In contrast, the tropical eastern Pacific was little chilled, and the Indo-Pacific region not at all.

These events, then, are the well-established background explaining the poverty of some groups of the Atlantic littoral today. They also indicate the generous amounts of time that have allowed Indo-Pacific and American faunas to diverge.

The weaknesses of the view of a continuous circumtropical fauna, in connection with *Uca* origins, are three. First, the mid-Atlantic barrier is almost as formidable for littoral animals with short pelagic larval stages as is the eastern Pacific barrier. Second, the consensus of thought now holds that no convenient land bridges extended even around the northern part of the Atlantic over which littoral animals could migrate. Granted that the northern seas and shores were much warmer then than now, it still seems unlikely that the Tethyan route was used importantly; although they were not subjected to known cooling, the species of East Africa and India are few in number. Finally, it seems again unlikely that only two genera and only advanced species of all this large family should be found in America, while all other genera and all the species showing most primitive characters are found only in the Indo-Pacific.

3. *The Panamic Region as a Possible Center of Dispersal.* If only the species numbers of present distribution were considered, the center of dispersal could logically be the crowded Panamic region. Even with no regard for geological history, however, this area is virtually ruled out as the center of origin on grounds of morphology and behavior. The vast majority of species in this richest area show characters which are specialized in comparison with those shown by 16 out of 18 species in the Indo-Pacific. These characters include carapace shape, armature of carapace and appendages, and social behavior patterns.

Again, out of 14 genera referred on good grounds to the Family Ocypodidae, only two—*Uca* and *Ocypode*—are found in the Americas. All others occur only in the Indo-Pacific, an area centered chiefly in the Indo-West-Pacific region.

Therefore, if the Americas, on the basis of sheer numbers of present-day species, are considered to be the center of distribution, these formidable objections exist: (1) They are all specialized forms, in comparison with the majority of Indo-Pacific forms. (2) All of the numerous related genera, with one cosmopolitan exception (*Ocypode*), are confined to the Indo-Pacific.

4. *The Possible Colonization of America via the Behring Strait.* This explanation of the present distribution of the genus seems most likely. The multitude of forms in America can be explained by the crossing and successful establishment of even a single Indo-Pacific species. The affinities of the migrants, of however many species, would almost certainly be with the root stock of the present subgenus *Thalassuca* (including *tetragonon* and *vocans*). Possible further affinities with *Australuca* (including *bellator*) are indicated if a second stock is involved. In the absence of a helpful fossil record, further speculation is inappropriate.

In the Eocene and during the early Oligocene, subtropical seas extended at least to the 55th parallel and a warm temperate climate far up into Alaska. Fiddler crabs are notably adaptable to cold weather, even within a single species and without external signs of subspeciation (*tangeri*, *seismella*, *polita*). It therefore seems the necessary crossing could have been made up the warm coast of east Japan, with time to breed along the bridge from summer to summer. For millions of years winters in that region may not have been as severe as in present-day Connecticut and southern Massachusetts, where three species now occur. All of these forms have close relations in the tropics.

If this hypothesis is correct, the migrants, once down the west coast of America, found an abundance of suitable habitats. Similar ecological conditions are found in tropical swamps, estuaries, and protected bays from Fiji to Zanzibar and from West Africa to Costa Rica. Yet nowhere in America, it seems likely, did many ocypodid members of the mangrove community then exist. The *Macrophthalmus*-like fossil of the Jamaican Pliocene (Rathbun, 1919) certainly has no present-day descendants. Conditions, for whatever reason—the absence of competitors or the presence only of those giving inferior competition—must have been ripe for a burst of speciation.

The second possible means of a migration from Asia is via island-hopping and the crossing of the East Pacific Barrier. A few years ago this route appeared discredited but, as discussed by Garth (1966), in some pelagic larvae the duration of instars can be prolonged, with obvious possible effects on distribution.

On the whole, then, the hypothesis is favored in this contribution that the origin of *Uca* was in the Indo-Pacific region and that one or two of the groups there gave rise, after migration across the Behring Bridge, or possibly the mid-Pacific, to the American species.

5. *Evolutionary Aspects of* UCA *Zoogeography.* Two American subgenera of *Uca* are morphologically closest to the Indo-Pacific stock. These are the subgenus *Uca*, including *maracoani* and the rest of the American "narrow-fronts," and the subgenus *Minuca*, erected for the specially broad-fronted spe-

cies. They, West Africa's *tangeri*, and the Indo-Pacific subgenus *Thalassuca* (including the ubiquitous *vocans* and *tetragonon*) clearly had common ancestors. In America, however, social behavior developed well beyond the *Thalassuca* activity patterns, along lines parallel to those found in any other waves of migrants, presumably of *Australuca* (*bellator*) stock (p. 435). Examples of such parallel social development even intergenerically are found throughout the family; the Indo-Pacific genus *Ilyoplax* is an excellent example (p. 494). From these advanced behavioral characters, as well as from strictly morphological traits, it is held here that *tangeri* is derived from the stock of the American subgenus *Uca* (*maracoani*, etc.), rather than directly from the Indo-Pacific *Thalassuca*.

Uca thayeri, for which the subgenus *Boboruca* has been erected, is of great interest from two points of view. As already mentioned, it is one of the few American forms in the genus which have changed so slowly in the past five million years that the forms on both sides of the Isthmus cannot logically be regarded as more than subspecies on the basis of the usual criteria. Second, this species shows combinations of characters, both morphological and behavioral, suggesting definite affinities with the Indo-Pacific narrow-fronts of the subgenus *Deltuca*.

The other species represented on each side of the Isthmus by forms considered of subspecific rank are (*Uca*) *maracoani* and (*Minuca*) *vocator*.

The remaining two groups of American *Uca*, placed here as the sole representatives of Bott's subgenus *Minuca*, include the most advanced species in the genus, both morphologically and in social behavior. Whether they developed from the same root stock as the subgenus *Minuca* (*rapax*, etc.), as seems most likely, or whether they represent a separate crossing, with their nearest relations among the ancestors of the subgenus *Australuca*, it is impossible to say.

Celuca has speciated most profusely in the tropical east Pacific, and it is from this group that the two Indo-Pacific species from American stock are derived (*triangularis* and *lactea*). Apparently they are descended from one or two successful westward migrations. This view seems more likely than the alternative, which would demand an Indo-Pacific origin for *Celuca*, making all crossings then from west to east. The closer affinities of *Celuca* are undoubtedly with the other American groups rather than with root stocks near the subgenus *Australuca*, the only candidates with relations among present-day Indo-Pacific crabs. The first hypothesis, then, demanding one or two east–west crossings, seems the more likely. The matter will be further considered in the last chapter.

Unless a mid-Pacific route was used, the crossings, like those made by the original migrants, would have had to be made before the onset of really cold weather. Only three of the contemporary forms in these groups extend into regions regularly subjected to temperate or upper subtropical winters. These are *pugilator* in the northeastern United States, *crenulata* in California and at the mouth of the Colorado River, and *lactea* in Japan, Pakistan, and southeast Africa.

6. *Conclusions Concerning the Origin and Distribution of* UCA. The hypothesis favored in this contribution is that *Uca* originated in the Indo-Pacific region, that ancestors of one or two of the Indo-Pacific subgenera there gave rise, after migration across the Behring Bridge, to four new subgenera in America; that representatives of one of these groups migrated westward via the same route and gave the Indo-Pacific fauna two living representatives of these advanced American subgenera. The chilling of the Atlantic can in part explain the paucity of Atlantic species compared with their abundance in the eastern tropical Pacific. The large tide ranges in the Pacific area may explain the wealth of recent species in that restricted region (see Chapter 2, p. 443).

D. SUBDIVISIONS OF THE INDO-PACIFIC REGION IN RELATION TO *Uca* DISTRIBUTION (Table 8)

No particular order of listing is very satisfactory, since the regions are related in different ways, depending on the species groups examined. Still, very definite conclusions can be drawn on the subject. A study of the list of Indo-Pacific species and their allopatric affinities to one another leads to the following statements. The most specialized forms, with no exceptions, are found along the Philippines–Java axis; the least specialized are peripheral, particularly in northwest Australia, the China–northwest Taiwan–Japan region, and, to a lesser extent, the mid-Pacific region. This is in contrast to the frequently existing condition in birds and other animals, where specializations occur in peripheral isolation or other conditions of partial isolation. The situation will now be examined in more detail.

Uca in the Indo-Pacific, as shown by the distribution of species and subspecies, indicate the division of the vast stretches of the Indo-Pacific into seven major subdivisions, as follows.

1. Northwest Australia (Dampierian Region).
2. China; northwest Taiwan; Japan.
3. Pacific Islands.
4. Northeast Australia and New Caledonia (Solanderian Region).
5. Philippines–East Indies Axis; New Guinea.
6. Northern Borneo; northern Sumatra; Malaya to eastern India.
7. Western India and eastern Africa.

Table 8 lists the species by regions and indicates allopatric relationships. Characteristics of their respective *Uca* populations are described below.

1. *Northwest Australia* (*Dampierian Region*). This area has two remarkable characteristics. First, of the eight species recorded, at least two are allopatric forms showing less advanced waving display characters than do their representatives in other regions. Second, except for *demani* and the three members of the typically Australian subgenus, *Australuca*, the affinities are definitely with the *Uca* fauna of the other coasts of the Indian Ocean, rather than with the Pacific faunas to the north and east.

2. *China; Northwest Taiwan; Japan*. The six species concerned (*acuta*, *dussumieri*, *arcuata*, *formosensis*, *vocans*, and *lactea*) are, with the exception of *dussumieri*, distinct forms with more conservative morphological and, where known, behavioral characteristics than have the neighboring forms in the Philippines–East Indies area. *U. dussumieri* alone is a surprise. Although it reaches seasonally cold Fu-chien Province, it belongs, according to all discernible morphological evidence, to the subspecies *spinata*. This form is found typically in the tropics, in Singapore, northwest Borneo, and the west coast of Malaya. At the present time only *arcuata* and diminishing populations of *lactea* occur in Japan. *Uca formosensis*, known only from northwestern Taiwan, is possibly a cold-water allopatric representative of the far-ranging species, *tetragonon*. More probably it is a conservative member of its subgenus (*Thalassuca*), with resemblances to *Deltuca*.

Species reported from the Nansei (Ryukyu) Islands have, with the exception of *arcuata*, proved to be identical with the tropical forms of the Philippines–East Indies axis; *v. vocans* and *lactea perplexa* are of usual occurrence; *d. dussumieri* is apparently an occasional stray, where it was probably reported as *dubia* by Stimpson (1858); specimens agreeing with his original description proved upon examination to be examples of *d. dussumieri*.

3. *Pacific Islands*. These are expectably characterized by a progressive impoverishment eastward. Only two species, *tetragonon* and *chlorophthalmus*, are found east to the Society Islands and beyond; *lactea* and *vocans* reach Samoa; *coarctata* filters out in Fiji. One of them, *vocans*, is a relative conservative among the six subspecies; *coarctata* and *lactea* cannot be usefully distinguished taxonomically from the advanced forms found in the Philippines–East Indies axis.

4. *Northeast Australia and New Caledonia* (*Solanderian Region*). This rich area is chiefly a southward extension across New Guinea of the Philippines–East Indies axis. It differs in three ways: first, some northern species are not present; second, typically Australian members of *Australuca* are strongly represented; third, two species, *vocans* and *bellator*, form separate subspecies here.

5. *Philippines–East Indies Axis; New Guinea*. This area, very rich in number of species, is the habitat of the most specialized subspecies, the specialization being shown particularly in genital morphology and display behavior. The region extends in general to include part of Sumatra in the west and New Guinea in the east. The *Uca* extending northeast into the Nansei (Ryukyu) Islands have all proved to belong to this fauna rather than to the section typical of the cold-current shores to the west (2, above). Several of the forms in New Guinea have affinities with, respectively, northwestern Australia (*coarctata flammula* in parts of West Irian), northeastern Australia (*vocans vomeris*), and the Pacific Islands (*vocans pacificensis*); both of the latter subspecies were found in eastern New Guinea and show evidence of hybridization. The other species all belong to subspecies occurring in Philippines and, in most cases, south and east of New Guinea as well.

6. *Northern Borneo; Northern Sumatra; Malaya to Eastern India*. This region was separated from the Philippines–East Indies region throughout the Pleistocene and much of the earlier Cenozoic by the Sunda Shelf. It forms an area slightly richer in species of *Uca* and other ocypodids than any other in the Indo-Pacific, but its subspecies are usually identical with those of eastern Africa. In other words eastern Africa is an impoverished extension of the shores of the Bay of Bengal. To the east the subdivision extends around the tip of the Malay Peninsula and up the coast to Thailand. The north coast of Sumatra, and northwestern Borneo are typically included.

7. *Western India and Eastern Africa*. This fauna is poor in species compared with the wealth of forms farther to the east. Only one species, *inversa*, does not have allopatric representatives elsewhere, or, like *tetragonon*, range beyond the region. The allopatric forms are all moderately to extremely advanced members of their respective groups either in genital morphology, waving display, or both.

8. *Areas of Coincidence*. One of the most interesting aspects of this entire study concerns the areas of coincidence in distribution. These occur in the general region extending from Ceylon and Madras around the tip of the Malay Peninsula (south of Penang), and in Sumatra, Java, Borneo, Celebes, and the southern Philippines. In these areas there is clear juxtaposition and in some cases evidence of hybridization in adjacent western and eastern populations. The groups involved are the subspecies of *dussumieri*, *vocans*, and *lactea*, each in a different subgenus, along with the full species *forcipata* and *coarctata* of the superspecies *coarctata* (subgenus *Deltuca*). All of this mingling might normally be ex-

pected through the classical lifting of a barrier. In this case the barrier, the Sunda Shelf, was removed by its flooding, probably most recently some 10,000 years ago. The situation is discussed under the species involved as well as in the chapter on speciation, p. 530.

9. *Conclusions.* It seems that the broad paleozoogeographical picture for the genus may be as follows. In the days of the maximum development of the Tethys, during the Cretaceous and early Tertiary, an access to its usually placid shores was available from the Australian shield all the way to China, India (then a great island), and a very small Africa.

The land of west Australia has been perhaps least disturbed, and its fauna therefore least subject to evolution since that time; particularly, it lacked the stimulus of true isolation. Also, its simple coastline provided relatively few habitats. The fauna of both west Australia and the China–northwest-Taiwan–Japan axis had eventually to adapt to moderately cold winter weather. This too, through decrease in numbers of generations, could slow evolutionary rates in comparison with tropical *Uca*, most of which breed through the year.

All the other regions, with the exception of the Java–Philippines axis, show various geological histories but are relatively lacking in striking events.

In contrast, the Java–Philippines axis starting in the Tertiary has undergone violent volcanic activity which continues to the present day. Coastlines have been changed repeatedly; islands have risen and subsided; shores are convoluted; a multitude of niches has appeared and vanished. All of this apparently proved highly stimulating to evolution in a genus of *Uca*'s requirements. The subspecies all show the most highly developed displays and the most complex gonopods in their species.

E. SUBDIVISIONS OF THE AMERICAN REGION IN RELATION TO *Uca* DISTRIBUTION (Table 9)

The dates of migration to and from North America must of course remain problematical. Because of lowered temperatures the movements could scarcely have occurred later than the Oligocene in either direction, in any use of the Behring route. If the first migrations eastward occurred in the Paleocene, and the last during the middle of the Oligocene, a period of some 30 to 55 million years was available for the development of American groups. When the changes are considered that have occurred in some allopatric species within perhaps the last five million years, after the closing of the American isthmus, it seems likely that the long, warm stretch of the early Tertiary was altogether adequate for the evolution of the new subgenera.

1. *Eastern Pacific.* In the eastern Pacific the distribution of *Uca* divides clearly into three zones. The first extends from the southern part of California and the mouth of the Colorado River to the southern part of the State of Oaxaca, in south Mexico; the second, from El Salvador and the Gulf of Fonseca to the southern edge of the Gulf of Guayaquil; and the third, from Peru south of the Gulf to northern Chile. In contrast to the supremely rich tropical subdivision, the number of species in the northern zone is mediocre. Garth (1960) has examined in detail the composition of the brachyuran fauna in the region, including *Uca.* The southern zone, down the almost straight west coast of Peru and northern Chile, is one of the most impoverished coasts in the world, from the point of view of support for populations of *Uca.* Not only is this third subdivision almost devoid of suitable habitats, but the coast is relatively cool for its latitude because of the Humboldt Current.

In the northern zone only one species, *crenulata*, is endemic. Two others are considered in this contribution to be subspecies of species occurring also in the south. None of the two or three species counted as questionably ranging south to Chile appears to differ from northern forms; recent material, however, is non-existent.

2. *Western Atlantic.* On the west coast of the Atlantic, four zones are counted. The first covers the temperate shore of the United States; the second those of the states bordering the northern part of the Gulf of Mexico; the third, tropical North and South America, including the Caribbean islands, as far south as Guanabara Bay in Brazil; the fourth, the extreme southern part of Brazil, adjacent Uruguay, and, from a single record, the northern shore of Argentina near the mouth of the Rio de la Plata.

In the northern zone three species occur farther north than anywhere else in the world and are regularly subjected to freezing winter temperatures. Their boundary at present is Cape Cod, although there is some evidence that one of the species once reached the southern part of Maine. The zone's southern boundary is northern Florida, where the three species of the north are supplemented during clement periods by two stragglers from the tropics, their presence favored by the Gulf Stream. The shifting and precarious footholds held by these southern forms correspond to the fluctuating distribution of several species in the Nansei (Ryukyu) Islands, which are similarly affected by the Japanese Warm Current.

The second subdivision is a rather anomalous zone, just beginning to be understood (Salmon & Atsaides, 1968.1, 1968.2). Here along the northern part of the Gulf Coast of the United States and northwest Mexico, three of six forms of *Uca* are somewhat different from their allopatric representatives, both temperate and tropical, on the Atlantic coast and on the southern part of the Gulf. Another interesting occurrence in the region is an endemic species, *subcylindrica*, from Texas and the adjoining coast of Mexico.

The five species now found in the southern half of Florida are of varied geographical affiliations in keeping with the intermediate and fluctuating climate of the area; consequently the region is not viewed as a subdivision. Three of the species are tropical and here, at the northern edge of their extensive ranges, only one seems well established. A fourth species is confined to the subtropics and the Gulf coast, while the fifth, although it thrives in south Florida, is characteristic also of the temperate coast to the north. A sixth species, wholly tropical, has not been reported for many years.

The third zone in the Atlantic covers the tropics more completely than in the Pacific, extending from the West Indies and the tropical part of Mexico to Rio de Janeiro, Brazil, at the Tropic of Capricorn. Even with 12 species, the subdivision supports only two-fifths as many as the more restricted tropical zone in the eastern Pacific.

South of the tropics, in the fourth zone, a single endemic species occurs. While distinct, with a short range from Rio de Janeiro to Buenos Aires, *uruguayensis* is clearly the allopatric representative of a widespread group of northern species. Five or six of the tropical species filter out not far south of Rio.

With the exception of *subcylindrica*, mentioned above, every form occurring in the western Atlantic has at least one close relation in the eastern Pacific.

3. *Conclusions.* A relative impoverishment of the Atlantic fauna in comparison with that of the Pacific shows strikingly when the numbers of species of *Uca* are compared on the two sides of the Isthmus. Two additional factors, besides the presumed influence of the Ice Age climate, should be kept in mind as possible contributory causes to the disparity in species. If, as seems most likely, the ancestors of American *Uca* migrated from Asia, then their first differentiations were likely to take place on the nearest Pacific shores, even if the Atlantic happened then, and often subsequently, to be fully accessible. Again, although a mangrove swamp in Venezuela or Brazil now appears as richly suitable for *Uca* as its equivalent in Costa Rica or Ecuador, differences in such complex biotopes, rather than climate, may have controlled in part the rate of speciation in the neighboring oceans.

F. SUMMARY

The 62 species of *Uca* recognized in this contribution occur throughout the warmer parts of the world. The majority are confined to the tropical eastern Pacific, while on all continents the warm temperate regions are impoverished, as is the entire coast of west Africa. It is considered most likely that the genus arose in the Indo-Pacific, and that the American species are descendants of migrants moving along the Behring Bridge during the early Tertiary. It is further suggested that one or two later migrations in the opposite direction gave rise to Indo-Pacific members of a subgenus otherwise American. In the Indo-Pacific region seven subzones are recognized, of which the richest are those included in the tropical areas from India to the Philippines and northeastern Australia. The development of allopatric species and of subspecies was clearly influenced strongly by the repeated emergences of the Sunda Shelf. The Sahuli Shelf also probably played a role, as has the associated orogenic activity that has been characteristic of the entire region. The most conservative area, judging by the morphology of the local *Uca*, has been the northwest coast of Australia, which has had a contrastingly quiet history during the Cenozoic, the presumed period of the group's evolution. Several zones are apparent in both oceans bordering the American continents, each of the series running north and south in conformity with the continental coasts. Aside from climatic factors limiting distribution, the most important events were the sporadic emergences of land bridges that partly or wholly divided the faunas of the Atlantic and Pacific; the current bridge, the Isthmus of Panama, has served as a complete barrier for perhaps five million years.

Chapter 2. Ecology

OUTLINE

A. INTRODUCTION

Almost all adult fiddler crabs live in the intertidal zones of sheltered bays and estuaries, digging and feeding in sandy mud and muddy sand throughout the warmer parts of the world. These habits show basic demands for tidal action, for a soft and nutritious substrate, and for warmth.

As usual in *Uca* biology, each of these needs turns out to have wide variability, and all illustrate well the capacity of the genus to adapt to a wide range of conditions.

In this chapter the chief physical and biological factors in their environments will be examined. Because of the overlapping and interdependence of categories, none of the usual groupings of ecological factors will be made. Instead, the categories presented range roughly from the most physical to the most biological in nature.

The ecology of *Uca* may be considered from two distinct points of view. The first of these aspects is the distribution of the species and the second the activity of the populations under various conditions. These divisions will be considered under each heading.

Since very little is known of the ecological requirements of the pelagic young, these stages will be mentioned below only incidentally.

General accounts of climatic factors, the intertidal zone, estuarine environments, mangrove associations, and chemical aspects of ecology will be found in appropriate textbooks and isolated papers. Particularly useful in providing background are Allee, Emerson, Park, Park, & Schmidt (1949); Hesse, Allee, & Schmidt (1951); Ekman (1953); Trewartha (1954); Day & Morgans (1956); Macnae (1956, 1957, 1968); Macnae & Kalk, eds. (1958); Moore (1958); Teal (1958, 1959); Edney (1960, 1961, 1962); Macnae & Kalk (1962); Bliss (1968); Bliss & Mantel, eds. (1968); Miller & Vernberg (1968); and Newell (1970).

Hedgpeth (1957.1, 1957.2) makes sensible comments on ecological terminology. Since, as he points out, there is still no close agreement, particularly internationally, on the use of new terms, it would be inadvisable to bar the use of such inexact but useful words as "environment," "habitat," and "community." He also suggests that when more technical terms are used they be defined at the time by each author.

Since even now ecologists do not seem all to be in perfect agreement on appropriate uses even of such established terms as "biotope" and "biocoenosis," less widely accepted words will be discarded here in favor of the simplest terminology consistent with lack of confusion. For example, "Intertidal Zone" will be used throughout to indicate the general habitat of all *Uca.* The zone will be divided into "upper," "middle," and "lower" portions, rather than into more precise subdivisions in which various prefixes are placed before the general word "littoral." Although the more technical terms are in other studies often preferable, their use here would be inadvisable, for two different reasons. First, we are still too ignorant of exact ecological needs in the genus. Second, many species have widely variable ecological distributions.

It is hoped that this use of a majority of non-technical terms will be acceptable even to professional ecologists, since the present treatment does not aim to present a technical account of the ecology of the genus. Desirable as such a contribution would be, too little work has been done by anyone to make it possible. As in many aspects of *Uca* biology, only a résumé can be given of the beginnings, along with key references, to serve as a basis for future work.

Finally, it is cheering to note that Hedgpeth's pleasant comment of some years ago (1957.2: 48) has suddenly gone out of date. He said: "There are many still unreconstructed people to whom ecology is an unnecessary synonym for natural history." Perhaps our technical knowledge of the ecology of fiddlers will swiftly grow because of our present realization of the overwhelming importance of the ecology of the planet. And the survival of many now endangered *Uca* populations may incidentally be prolonged.

B. TEMPERATURE

Fiddler crabs are typically adapted to warm climates. In the rainy tropics they are active all the year around, and breeding individuals are found during every month. In the subtropics reproduction in some species is restricted by the dry season, rather than by temperature. The few species found in the warm temperate zone, however, are strongly controlled by temperature, both in the limits of their distribution and in their seasons of activity. In these forms reproduction is confined to the warmest months, while during cold weather the crabs hibernate in burrows.

1. *Geographical Ecology and Temperature.* The world climate map given by Ekman in the English edition (1953) serves admirably for discussion of *Uca*'s distribution in relation to temperature. The simple zonation is in keeping wtih the distribution of this genus, as with that of other littoral forms. Three of its main divisions cover *Uca*'s range—tropics, subtropics, and the warm temperate zone. The complex subdivisions required in terrestrial climatology are inapplicable to this intertidal group.

2. *Low Temperatures.* The lowest levels at which temperate and subtropical populations display vary widely. For example, in the latitude of New York City (42° N) in mid-June, *minax* fed and moved about above ground during periods of low tide. Yet the crabs did not display on days when the weather bureau temperature during the preceding night fell below 21° C (70° F); this behavior occurred in spite of the fact that daytime temperatures regularly reached above 29° C (84° F). The readings were made on sunny days with the instrument held barely clear of the ground and shaded.

During 1968, a series of temperature readings was taken on the southern coast of Cape Cod in the northeastern United States, a peninsula marking the northern limit of *pugilator*. The nightly minima were read from a point just above high-tide level, with the base of the frame of the maximum-minimum thermometer in contact with the ground, and the instrument sheltered by a post on one side and a piece of wood above it. The diurnal readings, obtained as in *minax*, were all made in the midst of the observation area. During June the nightly low ranged from 7° C (44° F) to a single reading of 15° C (59° F), while the daytime highs, regardless of sunshine, lay between 9° C (49° F) and 29° C (84° F). On June 1, a sunny day, several individuals waved at low intensities when the temperature stood at 19° C (66° F), the low of the previous night having been 10° C (50° F). Although similar records were made several times later in the season, they mean little from a functional viewpoint, since the waves were not fully developed and no other trace of social behavior of any kind was seen. The season's maximum amount of social activity, including presumably actual breeding, occurred in the middle weeks of June, the population being notably less active in July in spite of higher temperatures. The July lows ranged from 7° C (44° F) on July 30 to 21° C (70° F) on July 18; the highs extended from 22° C (72° F) to 31.5° C (89° F). At no time during the season did the level of social activity in the species appear equivalent to that found in more southern populations.

In comparison, on the west coast of Australia, at Broome (17° S), four of the five local species were active socially in early May, the Australian autumn, although the temperature nightly fell to the neighborhood of 15° C (59° F); the days, however, were tropically warm.

It is probable that in subtropical localities near the temperate zone, such as Florida, Rio de Janeiro, and the north Philippines, populations of truly tropical species are usually killed off by the occasional freezing temperatures. In these cases the populations are doubtless quickly replaced through the arrival of pelagic larvae, carried by currents from more tropical regions.

Edney (1962) found in the laboratory that temperatures of 10° C (50° F) were lethal for all the South African specimens with which he worked, the material having been taken on Inhaca Island, Mozambique. In July and August the island's temperature in the mangrove water sometimes falls to 17° C (62.6° F) (Macnae & Kalk, 1962). Although, as Macnae (1957) says, the species of *Uca* on Inhaca are all tropical, still these populations are clearly tolerant of mildly subtropical temperatures.

Physiological studies by a number of investigators (Miller & Vernberg, 1968, and refs.) show that low temperatures are directly important in limiting the distribution into temperate latitudes of this essentially tropical genus. For example, the tropical crab, *r. rapax*, acclimated to 18° C (64° F) in the laboratory, soon succumbed to a temperature of 10° C (50° F), although this temperature is readily tolerated by its close northern relation, *p. pugnax*, with which, in the northern half of Florida, it is sometimes sympatric. Unusually low temperatures also interfere with growth, molting, and other processes in both larvae and adults.

Several species—*crenulata* in the eastern Pacific, *rapax* and *thayeri* in the western Atlantic, and *tangeri* in southern Europe and West Africa—range from the deep tropics through the subtropics and well over the border line of the warm temperate zone without apparent morphological changes.

Still, behavior differences related to temperature are notable in these species ranging widely through climate zones. In the tropics, *rapax* is socially active perennially in all except the driest periods; in the subtropics seasonally; and in the warm temperate zone activity is controlled largely by temperature.

Temperature directly controls the speed of display in subtropical populations, as in *tangeri* (Altevogt, 1959).

3. *High Temperatures.* According to my observations (unpublished), it seems highly probable that the four forms of *Uca* that remain active at the highest temperatures are Red Sea populations of *tetragonon*, *vocans hesperiae*, *inversa inversa*, and *lactea annulipes*. Of these, work at Massawa showed that *tetragonon* proved most resistant to heat, continuing to wave in full sunlight when the mercury reached 41° C (106° F) in the sun at the surface, providing there was an intermittent breeze. With or without a breeze, *tetragonon* always descended its burrow at about 42° C (108° F). At 41° C (106° F) *lactea* was inactive, in its burrow. The other species descended at about 40° C (104° F), although display and courtship stopped at 39° C (102° F). Feeding and threat stopped earlier, at about 38.5° C (101° F). In contrast, most *Dotilla* and all hermit crabs descended by 38.5° C (101° F.). In Singapore, where maximum ambient temperatures are lower than in the Red Sea, the temperature tolerance of *U. lactea* was lower by 5.5° C (almost 10° F).

Species of the subgenus *Celuca*, the group best adapted for land, best withstand the highest temperatures, whether in the Indo-Pacific, eastern Pacific, or western Atlantic. The dazzling display whitening assumed by a number of these species may help keep the body temperature down, but whitening is by no means found in all hot locations or in all the expectable species. The extreme of whitening also occurs sporadically in *Thalassuca* and *Uca* and does not seem to be related to their endurance of heat during display, although it well may prove to be a factor.

It must be remembered that two temperatures are important to all—that on the inside of the burrow and that on the surface outside the mouth. The inside temperature is of course less extreme in each direction. At Massawa in July, when surface temperatures were about 42° C (108° F), four inches down the burrow the reading was only 40° C (104° F). Extreme readings on a breezeless protected flat were 43.5° C (112° F) on the surface, and 40.5° C (105° F) four inches down in the burrow of an *inversa.*

Macnae has shown that because of transpiration body temperatures in *Uca* in the open sunlight are 1° C or more lower than the air temperatures (1957).

The same author, always working on Inhaca Island in Mozambique, found that the upper limits of tolerance varied with the species, the individual, and even the season. In the Mozambique summer (January) toleration was roughly 2° C higher than during the winter. Nevertheless, 45° C (113° F) was lethal for all fiddlers. Of these *inversa* was notable for more tolerance than the rest; *lactea annulipes* followed; next came *vocans* and *chlorophthalmus*; *urvillei* was least tolerant of heat. The order is expectable in view of the habitats, *inversa* occurring usually on baking salt flats protected from sea breezes, *urvillei* often in the shelter of partial mangrove shade, and the others variously between. The habitat of *vocans*, near low-tide levels in very damp ground, would reduce heat exposure.

Verwey (1930), Orr (1955), and Teal (1958) found somewhat similar lethal upper temperatures.

The most direct climatic comparisons in acclimatization are those of Vernberg and Tashian (1959). They compared temperate and tropical American species, finding that at 42° C (107.6° F), or 44° C (111.2° F) tropical species survived longer than temperate forms. If the tropical forms were kept first for seven days at 15° C (59° F), the difference in survival time disappeared. Temperate zone species, as mentioned in the preceding section, were more cold resistant than tropical forms.

A biological clock mechanism seems to be concerned in the relation of seasonal temperature to display. Specimens of *U. arcuata* brought alive to the William Beebe Tropical Research Station in Trinidad from south Japan in May lived about 18 months. Individuals displayed well through the first and second summers, but did not display at all during the intervening winter, even though temperatures remained tropical, differences in day length were only very minor, and no dry season conditions were in evidence in the out-of-door crabbery. Unlike the winter behavior of the crabs in Japan, however, whether they hibernated partially or altogether, they fed and moved about normally in Trinidad and showed some territorial threat behavior. As said above, they did not wave and no courtship or mating seems to have occurred. Observation was not constant and if waving occurred very rarely it might, of course, have passed unnoticed; it could not however have taken place frequently.

C. Water

1. *Tides.* As in many marine animals, in *Uca* a direct relation exists between the number of species and the breadth of the tidal range. This relationship exists only of course where climate and substrate are suitable and geographical and historical factors appropriate. Even though *Uca* rarely takes advantage of the lowest tidal levels, wide intertidal bands encourage so many forms of life that these filter-feeding crabs, living on the middle and upper levels, undoubtedly benefit from the biological richness of the general environment. When more is understood both of their food requirements and of the actions of pheromones, the interdependence of factors will be better understood.

Whatever the detailed causes, more species live in the neighborhood of the Gulf of Panama than anywhere else in the world (Map 1). This region is notable for extremely wide tidal ranges. In the region of Tahiti the usual 6-inch tides can only be partly blamed for the presence of only two species, since this area is on the extreme edge of the East Pacific Barrier; few kinds of pelagic larvae from the west have been able to cross the long stretches between islands. In southeast Asia and the Philippines another major factor is doubtless responsible for the relatively few *Uca*, in addition to mediocre tides. This factor is the use of niches by other genera in the family not found in America (*Ilyoplax*, *Scopimera*, *Dotilla*, and others). In the tropics of the western Atlantic, which would normally make a good comparison with conditions across the Isthmus, the effects of the glacial epochs are no doubt still being felt (p. 433).

The tide, whatever its range, has a powerful effect on the activity of *Uca*. Usually, of course, the crab spends the entire period of high tide underground, emerging only after the water has receded from the level of the burrow's mouth. With the exception of unusual local populations of *burgersi* (p. 168) and *pugnax* (unpubl.), I know of no record of *Uca* performing waving displays, or engaging in combats or courtships underwater. Occasionally fiddlers feed when beyond the edge of the tide, or in shallow runoffs coursing through flats or lagoons; usually their eyes project above the surface. Often they escape threats by running a short distance into the water when they are at a distance from their burrows. Otherwise, they habitually stay away from the sea and descend their burrows as the tide advances.

Endogenous tidal rhythms play important parts in the activities of fiddlers. The rhythm is apparently fixed for an individual in accordance with the tidal schedule in effect at the locality where the postmegalops comes ashore, although, as usual in biological rhythms, the rhythm can be altered within a few days.

2. *Rainfall.* Rainfall is of special importance in bringing about high activity, including display, in fiddlers living near high-tide levels. These populations occur on the banks of tidal streams and especially on tidal flats reached only by spring tides. In periods of drought crabs remain in their burrows for days, weeks, or months at a time. The first showers bring them out to feed actively; within a week or less most of them start display and courtship. In the dry season even populations of the same species, such as *rapax* in the West Indies and northern South America, which live close to the shore and are exposed to regular semi-diurnal tides, do not display or breed during the dry season, although they feed regularly and are otherwise active. This seasonal activity in well-watered populations indicates the existence of still another biological clock.

Other good examples of this behavior occur in the same subgenus, *Minuca*, on both sides of the Isthmus of Panama; in both regions the dry season is severe and only the highest tides reach the flats. In the rainy season these localities show high activity daily, regardless of the tidal level.

In temperate zones warm temperatures and the rains usually coincide, as on the east coast of America and in southern Japan. A major reason for the poor *Uca* representation in California, where only *crenulata* occurs, is perhaps the fact that here the rainy season comes during the colder weather.

D. Salinity

Fiddler crabs, both as species and as individuals, are highly tolerant of changes in salinity; a review of the complex means by which osmoregulation is accomplished in *Uca* and other semi-terrestrial decapods is given by Bliss (1968). This adaptability is unsurprising, since so many species live under estuarine conditions which entail an impressive range. The extremes extend from salinity near or equaling that of the open ocean, characteristic of the dry season, to water which is practically fresh, in delta country during the height of the rains.

On the other hand, in many localities rich in *Uca*, testing shows that even during the height of the rains the water at high tide is almost equivalent in salinity to that of the nearby sea. Such a locality is found near Port of Spain, Trinidad. Another stabilizing factor of great importance is the frequently poor drainage in the burrows; a result of this condition is that the salts are held in the substrate, the burrow water showing a notably higher salinity than the tidal waters flooding the area. Hence, when crabs descend into their burrows to replenish the moisture supply in their gills, they do so from the standing water of high salinity, and so conserve their own supply of salts.

The tolerance to changes in salinity does not mean that salinity preference is not a species-specific characteristic, regardless of the breadth of the range. All *Thalassuca* and most *Celuca* live close to the open sea, where waters at high tide at all seasons approach in salinity those of the adjacent ocean. In contrast, *Deltuca* and *Minuca* in their respective hemispheres are tolerant of extremely low salinities, descending to about one part per thousand.

Abnormally high salinity appears to be intolerable. When the straits between the mainland and the island of Singapore were blocked by a causeway built soon after 1945, the adjacent shores became grossly impoverished. In contrast, in the experience of Dr. M.W.F. Tweedie, they had formerly been a rich habitat for many ocypodids. It seemed to both of us, when Dr. Tweedie showed me the locality in 1955, that the heightened salinity must have been the key factor in the decline of *Uca*. At that time it was about 40/00; the area did not appear to Dr. Tweedie to have changed very much in other ways, the human population had not notably risen in the neighborhood, and no pollution was detectable.

One of the areas of highest salinity inhabited by fiddler crabs is the Red Sea. At the surface of the open sea the salinity ranges from 37/00 to 40/00 (Ekman, 1953). Since at Massawa, where I worked, there are no backwaters where *Uca* are found, these salinities are probably fairly typical of the shore.

E. LIGHT

Fiddler crabs are primarily diurnal animals. Most of their activities, including feeding, digging, fighting, display, and mating, usually take place in daylight. This rhythm is particularly strong in tropical species, in which nocturnal activity seems to be confined chiefly to a little feeding by moonlight, to warning sounds made in periods of alarm within the burrows, and to wandering by crabs in the appropriate phases (p. 504). Nevertheless, as found by von Hagen (1970.3), nocturnal activity even in the tropics is clearly more plentiful than I formerly believed.

In the temperate zone, however, considerable courtship activity is nocturnal in both species investigated in detail. These forms are *tangeri* in southern Spain and north Africa, studied by Altevogt (1959, 1962) and von Hagen (1961, 1962), and, in the eastern United States, *pugilator* as shown by Burkenroad (1947), Salmon & Stout (1962), and Salmon (1965). It may well be that the shorter breeding season available in the north has resulted in selection toward nocturnal activity. This subject will be continued in a later chapter (p. 502).

It is certainly true that all populations of *Uca* show more waving activity in sunshine than in cloudy weather, providing only that the temperature is not too high (p. 442). Regardless of adequately warm temperatures and low tides, intensive feeding does not start in tropical populations until about two hours or more after sunrise. Display starts even later. At the end of the day, however, there is a higher tolerance for lower light levels than during the early morning. In an active population, both display and feeding are sometimes continued late in the afternoon, when low tide falls at that time near new and full moons. Sometimes waving activity then continues until sunset or even slightly later, as found in *vocans* near Bombay by Altevogt (1957) and in *vocans* and *lactea* in Fiji by Crane (unpublished).

F. THE INTERTIDAL HABITAT

The general habitat most characteristic of *Uca* lies in the tropics, somewhere near the mouth of a silt-laden stream. The stream flows into a sheltered bay partly fringed by mangroves. Beyond the mud flats near the river mouth, along the shores of the bay, curve wide beaches of sandy mud and muddy sand. Tidal lagoons often fill depressions behind the shore. Sometimes the locality consists only of a narrow stream as it flows from nearby hills into a small bay on an island's lee. Sometimes it embraces the vast delta of one of the great rivers of the tropical world.

As shown in Figs. 21-23, almost all species of *Uca* live in some part of this general habitat. Only a few forms occur either in more exposed localities or far upstream in altogether fresh water.

In particular, no *Uca* live on surf-beaten shores, pure sandy beaches, rocky shores, or in tide pools. Two species are borderline exceptions. One is *tetragonon*, which in some localities is found only on shores where a thin layer of sandy mud covers a firm substrate of coral and shelly conglomerate. The second is *panamensis*, found only among stones at the ends of sandy mud beaches.

No *Uca* live in the middle of broad open flats of soft, deep mud, probably because the deficiency of oxygen causes a food shortage. Only *maracoani* and a related form, *ornata*, extend far out in such mud. Even they do not inhabit its middle portions. Finally, no *Uca* live in the deep shade of thickly growing mangroves.

In brief, fiddler crabs may be viewed as animals living in environmental borderlands. Just as many birds and butterflies occur typically on the edges of fields and forests, so *Uca* is adapted not only to the major boundary between land and sea, but within that tidal zone to the edges of rivers, mud, and mangroves.

G. BIOTOPES

The term *biotope* will be used to denote the subdivisions of the general *Uca* habitat described in the preceding section. This is characterized by Hesse, Allee, & Schmidt (2nd edition, 1951, p. 165) as "an area showing uniformity in the principal habitat conditions."

In a discussion of *Uca* at the present time there seems to be no advantage in subdividing the biotopes listed below or in grouping them into larger units. This conclusion has been reached simply because we do not yet know enough about factors that limit particular species of fiddler crabs to special sections of the shore. For example, food requirements are for many species undoubtedly an important limiting factor of which we now know practically nothing.

Because of these uncertainties, the 16 biotopes proposed for use are listed with no suggestion of hierarchies. It is certain, however, that all are not of equal importance and that they are not sufficiently subdivided. Nevertheless the list should prove of distinct pragmatic value, since it is based on wide personal experience in observing the ecological distribution of species in the field. Figures 21-23 and Table 10, used in conjunction, give an overall view of the occurrence of *Uca* as it is now known. Further details will be found under the species headings in the systematic section.

The list below gives the outstanding superficial characteristics of the biotopes. They are numbered in accordance with the above-mentioned figures and table. The same numbers are used in the species descriptions in the systematic section under the heading Biotopes.

List of Intertidal Biotopes

1. (Surf-battered rocky shore: no *Uca.*)
2. (Rocks and tide pools: no *Uca*, except for *panamensis*, which rarely occurs in tide pools.)
3. (Unprotected sandy beach: no *Uca.*)
4. Stony sand with underlying mud, ranging sometimes to a hard substrate of coral or shelly conglomerate, with mud in interstices and overlying the surface in a thin layer.
5. A thin layer of sand overlying mud.
6. Muddy sand to sandy mud.
7. (Open flats of soft, deep mud, far from shore, or middle portion of a broad, protected expanse of similar mud: no *Uca.*)
8. Open mud flats near mangroves.
9. Muddy sand to mud, partly shaded by edge of mangroves.
10. (Mud in full shade of dense mangroves: no *Uca.*)
11. Flats of muddy sand, sandy mud, or mud in or close to mangrove-fringed lagoon; some of these flats are flooded only by occasional spring tides.
12. Muddy stream banks, flats, near mouth; close to mangroves.
13. Same as no. 12, but with steep banks.
14. Same as nos. 12 and 13, but water brackish.
15. River banks, usually steep, upstream from mangroves; substrate muddy, clayey, or partly sandy; water ranging from almost fresh to fresh.
16. Subtropical and temperate marshes (mangroves absent).

Mud may be defined according to Macnae (1957) in the definition which seems best to fit the current situation as "mineral alluvium mixed with organic matter." Sand, on the other hand, is almost pure mineral matter, composed of particles larger than in mud, and to which consequently far less edible matter sticks. The mouth-parts of *Uca* are well adapted to these differences. The normal habitat of a given species, whether sandier or muddier, can be guessed merely by examining the setae on the endites of the second maxilliped; the more spoon-tips, the more nearly sandy the environment will prove to be (morphology, p. 455; behavior, p. 456).

Pheromones, secretions deposited by animals externally, may form a valuable part of the *Uca* environment. Their roles are not yet known in this group.

H. COMMUNITIES

Animals and plants associated with *Uca* would make a formidable study all by themselves. Macnae has contributed most to the subject in his reviews of South African fauna from ecological viewpoints (1956, 1957) and in his general account of mangrove flora and fauna of the Indo-west-Pacific region (1968). The present review will be confined to general comments. In the systematic section remarks are included under most species headings on their associates within the genus *Uca*, in both the broad and narrow uses of the word "sympatric."

1. *Associated Vegetation.* Mangroves are the most typical plant formation associated with *Uca.* When one approaches an unfamiliar tropical coast by land, sea, or air, the best way of locating *Uca* as rapidly as possible is simply to watch for the patch of mangroves lying nearest to the town and proceed there promptly at the next low tide. Mangroves, of course, consist of a variety of superficially similar trees and shrubs living in association, both the genera and species varying in different parts of the world. Two of the most common genera are *Rhizophora* and *Avicennia.* The stilt-rooted plants are found throughout the tropics and subtropics of the world, except on coasts so arid that there is neither a reliable rainy

season nor streams running into the sea. They are also absent from mid-Pacific islands. Their latitudinal range is similar to that of corals, extending from about lat. 32° S in southeast Africa to Bermuda (32° N), an exceptional northern record. Although *Uca* do not rely directly on mangroves for either food or shelter, they are of great indirect importance to the genus. The rotting leaves and associated animal life enrich the surrounding mud and muddy sand in which they grow and from which the fiddler crabs strain their food.

When the water becomes too fresh upriver for mangroves to grow, their place is taken in fiddler ecology by assorted plants, of which a good example in the American tropics is the arum *Montrichardia arborescens* ("mucka mucka"; "boroboro"). *Pandanus* serves similarly in many parts of the Indo-Pacific, such as in the great rivers of Borneo.

In temperate climates, too far north for mangroves, grasses are the principal substitutes. *Spartina* and *Phragmites* are good examples in the northeastern United States.

2. *Animal Associations.* (*a*) PREDATORS. The principal enemies of fiddler crabs among mammals are the crab-eating raccoons of the neotropics; their footprints are unmistakable. In the Georgia salt marshes of the United States, Teal (1958) found that raccoons and clapper rails both fed regularly on fiddlers, while aquatic predators of possible importance included fish and large crabs. As a whole, birds do not seem to take much advantage of the vast numbers of fiddlers that are sometimes available, although on any suitable shore occasional birds, ranging from herons to crows, attempt to seize a few members of the genus. Usually such hunters are so infrequent that they are negligible nuisances during observation of fiddler behavior.

In January 1971 near Bathurst, Gambia, John Endler listed the following predators of *tangeri*, along with their methods of hunting (personal communication): reef heron (eats adults in water); lemon black-backed gull (lies in wait for adults); ringed plover (stalks adults and young); whimbrel (stalks adults and, especially, young); crested lark (pounces on young in short flights); hooded vulture (lies in wait for adults). In addition he found that lizards (*Agama*) stalk the juveniles. This is the most extensive list I have ever seen that was compiled in one locality; comparison material from other areas would be of great interest.

Raut (1943) also observed whimbrels catching fiddlers, in this instance on an island near Bombay. The whimbrels' method of capturing the crabs has already been described (p. 4).

Kingfishers use still another technique. Unlike a whimbrel, which seizes a fiddler by the large claw, a kingfisher grasps the body. In both New Guinea and Ceylon I watched such a capture. The bird, crab in beak, flew with it to a perch, shook the fiddler vigorously until the major cheliped autotomized, and then swallowed the crab; in each case I picked up the claw and checked that the prey was a good-sized adult of *vocans*. One year at our mountain station in Trinidad the population of our most isolated crabbery suddenly declined; we found that a local kingfisher had learned to wait during our artificial low tides, and pounce.

In Trinidad and Venezuela I have also seen scarlet ibis seize fiddlers, but was not close enough to observe details of their technique. For these birds as well as for other species, the crabs seem usually to descend their burrows too quickly for capture. The successes for birds, perhaps, are usually insufficient to encourage the necessary effort. Possibly the crabs are distasteful, but we have no evidence whatever that this is so. Only among certain Indo-Pacific species are the crabs so vividly colored at all ages that aposematism may be suspected (p. 469).

Von Hagen (1969) reports that in Trinidad a grackle and a poecilid fish seized eggs from females of *vocator*.

The fish *Periophthalmus* has not been seen to attack *Uca*, although I have watched them often in association. The two animals frequently share a mud flat under crowded conditions; they appear to disregard one another entirely.

In southern Spain and Portugal, man is a direct predator of fiddlers, since *tangeri* claws are "harvested," the crab being thrown back to grow another (p. 118). Furthermore, in southern Japan a limited supply of canned *arcuata* is seasonally available (p. 44). Elsewhere, fiddlers do not seem at present to be eaten regularly by man.

(*b*) ASSOCIATED INVERTEBRATES. The most typical completely sympatric associates in the Indo-Pacific are grapsid crabs and other genera of ocypodids. Particularly notable are *Ilyoplax*, *Scopimera*, *Dotilla*, and *Macrophthalmus*. Outside the grapsoids are a few xanthids, hermit crabs, and small mollusks and worms, all of which no doubt contribute importantly to the biological richness of the substrate. On American shores other ocypodids are absent except for *Ocypode*, which overlaps with *Uca* only marginally.

(*c*) EFFECT OF MAN. Human activities are undoubtedly and strongly affecting the distribution and existence of *Uca*. A surprising result is that some of these effects are in favor of the fiddler crabs.

For example, a dock-side cove beside the Pacific entrance to the Panama Canal may be contrasted with a river mouth on the west coast of Palawan—one of the most undisturbed coasts in the world. The Panama spot, arched around the outlet to a large sewer, supported a cluster of straggling mangroves, received a wealth of garbage tossed there from time to time—and nourished more kinds of fiddlers than any other spot I ever found. Sixteen species lived in an area of less than four hundred square yards. The place has long since been ruined by oil and eclipsed by construction, yet the principle it illustrates remains unchanged. In general, the richest site for fiddlers will not be a shore devoid of humanity, but some spot close to a city, and even closer to a thriving village—preferably with stilt-legged huts and no plumbing.

In contrast, northwest Palawan was the worst tropical place of the kind for fiddlers in my experience, although it seemed ecologically ideal. The coast was wild, warm, humid, and rich with streams, mud, sandy mud, and mangroves. The whole shore was backed up by dense forest, and there was no trace of any source of pollution.

The negative side of man's activities is altogether expectable. Pesticides, roads, harbors, airports, swamp drainage, factory pollution, oil dumped from ships, overcut mangroves, and sheer numbers of people are all having drastic effects on fiddlers. These changes are so rapid that they can be detected with ease when one revisits a site only a short time later. The Panamanian cove mentioned above is an example. Another is a neighborhood on Singapore Island, formerly known as Pandan Swamp, which, during 1955, was a wonderfully rich locality for numerous kinds of ocypodids. The day I left, in September, workmen began to cut its mangroves to make still another useful fish pond. I hear it is now a thriving suburb.

In 1962 I could find no trace of *dussumieri* in Semarang, Java, which was its type-locality, while fiddlers of all kinds were, if still present, inaccessible anywhere near the great city of Djakarta, which was well known (as Batavia) in Dutch records of *Uca* during the past century. These days military installations screen almost all the city's shores and the burgeoning population has overrun the rest.

Although the southwest coast of India, near Cochin, has a topography and climate ideal for *Uca*, only two species occur there. In 1965 very small populations were found. The pressure of humanity has probably been severe here not only for a few years but for centuries.

Near New York City, on the New Jersey meadows, fiddlers seem to be extinct; fortunately populations at present remain in relatively accessible spots on Long Island and in Connecticut.

Still more fortunately, rivers still flow in the tropics—in Malaya and Brazil, in Borneo, Ecuador, and Costa Rica—where *Uca* still thrive. William Beebe once called a Venezuelan mangrove delta "the Land of a Single Tree." Thanks to the mangroves' inhospitality to man, each delta is also the land of a million fiddlers.

I. SUMMARY

Most *Uca* live in warm climates along the sandy mud shores of protected bays, the waterways of mangrove swamps, sheltered flats near river mouths, and the muddy banks of tidal streams. On the other hand fiddlers are never found on sandy beaches, rocky coasts, coral reefs, or any shore regularly exposed to strong surf. Aside from these limitations, their adaptability is worthy of respect. Both as species and individuals they can adjust to wide ranges of temperature, moisture, and salinity. In New England and Japan several species hibernate. In excessive heat fiddlers everywhere descend their burrows, whether in the middle of a tropical day or, in a state of aestivation, for many weeks in response to heat and drought. Nevertheless species-specific differences are increasingly apparent, not only in physiological tolerances but in the temperatures at which normal feeding and social activities occur. Tides are another important factor in *Uca* ecology; wide amplitudes encourage the development of a flourishing intertidal community, including *Uca*, when other conditions are sufficiently favorable. The activities of fiddler crabs are closely meshed with tidal rhythms, the crabs remaining in their burrows throughout the periods of high tide. After a drought rainfall stimulates social activity, although fiddlers go underground during a hard rain. All species are most active in bright sunlight, especially socially; at night waving display is always absent but sound production sometimes increases. Predation on *Uca* is limited, considering the abundance of both crabs and shore birds. Man, in progressively polluting and destroying habitats, is as usual the chief enemy. Except near large cities, however, fiddlers in the tropics seem to be holding their own.

Chapter 3. Structures and their Functions

OUTLINE

A. INTRODUCTION

In live fiddler crabs structure and function are challenging subjects that continue to provide biologists with a series of surprises. This chapter concerns selected morphological characteristics and their relations to certain ecological requirements and behavior patterns.

Most of the characters discussed are external and include all of those most typical of the genus. Where our knowledge is severely limited, as with antennae and antennules, the structures are briefly mentioned to underline our ignorance. The survey includes the range of variation, post-larval development, apparent adaptive values, and the functional relation, in social behavior, of the parts to one another. Descriptions of characters of taxonomic importance are given in the systematic section, beginning on p. 8.

While gills and mouthparts are superficially reviewed, internal anatomy, its physiology, endocrinology, and the bases of biological rhythms are omitted as outside the scope of this book. Key contributions, with references, include Barnwell (1968.1), Bliss & Mantel, eds. (1968), Démeusy (1957), Hoffmann (1971), Passano (1960), Sandeen (1950), Teal (1959.2), Vernberg & Tashian (1959), Waterman, ed. (1960, 1961), and Newell (1970).

B. THE CRAB AS A WHOLE

Male fiddler crabs stand out among all other animals in their general appearance, and a human observer can recognize them instantly, even when they are sitting motionless on a tropical mud flat among a bewildering throng of other small crustaceans. Their outstanding characteristic is the contrast between the two chelipeds, one being strikingly large while the other is minute; no other group shows a comparable disparity.

In other respects, the shapes of all *Uca* resemble those of many other shore crabs. The carapace is usually smooth and always convex, with roughly four to six sides. Its divisions are not deeply set off from one another, although sometimes the branchial regions project well above the dorsal surface. The eyes are on stalks. The eight walking legs in an overall view are not remarkable.

When any *Uca* is examined closely, the prevalence of tubercles, serrations, ridges, and furrows is striking. They occur especially on the sides of the carapace, around the orbits, on both chelipeds, and on the ambulatories. They divide functionally into two groups. Those on the minor cheliped and on the more proximal segments of the major cheliped and ambulatories rub against the carapace or against one another during agonistic situations. In contrast, the manus and chela of the major cheliped and at least the mani and dactyls of the ambulatories are used primarily in ritualized combat, engaging with correlated structures on the opposing crab. The continuing discovery of unsuspected uses of armature details remains one of the great surprises in the study of fiddler crabs.

C. SIZE AND ALLOMETRIC GROWTH

Size is of special interest in fiddler crabs because parts of their anatomy grow at very different rates. The large claw, especially, is far longer in large individuals than in small adults of the same species. As a result its development has often attracted the attention of observers, who have ranged from curious naturalists to biologists studying growth in a variety of animals. The general term allometric growth is currently applied to such an inequality of rate. Gould (1966: 629) defines allometry in part as ". . . the study of proportion changes correlated with variation in size of either the total organism or the part under consideration . . ."

No detailed contribution to either size or allometry in *Uca* has been attempted in the present study. The following paragraphs give only a summary of the range of sizes in the genus and of their distribution among the subgenera, along with a brief introduction to their growth ratios. All measurements in this section are in millimeters.

The fiddler crab with the largest dimensions known to me is a specimen of (*Afruca*) *tangeri* from West Africa in the collections of the American Museum of Natural History; its carapace measures 33 long and 47 broad, while the propodus attains 109. The next largest is a (*Uca*) *maracoani insignis* I took in Ecuador, measuring 31.5 long with a propodus of 94. Probably individual *maracoani* in life surpass in weight *tangeri* of equal carapace lengths because of the greater breadth of each finger of the claw.

The smallest *Uca* of mature proportions is (*Celuca*) *batuenta*; the largest individual known, the holotype, measures 4.8 long and 7.6 wide, with a propodus of 11.8. Two other species, (*Minuca*) *pygmaea* and (*Celuca*) *tenuipedis*, are both known only from specimens less than 6 long; all three are from the tropical eastern Pacific, the region characterized by the small size of most of its numerous species of fiddler crabs (pp. 533, 534).

Between these groups of extremes small species are far more numerous than large, as shown by the chart below. It is furthermore true that the largest sizes within a species are rare, the most numerous and active members of a breeding population usually being considerably shorter. Because longer individuals not only have much longer claws than short crabs but are proportionately broader and thicker as well, a slightly longer crab is of much greater bulk than is indicated by the length dimensions of the carapace and appears much larger in the field.

These differences can be of great importance to an investigator when he is selecting species for various kinds of research, ranging from neurophysiology to behavior observations in indoor crabberies; further comments on these practical aspects will be found in Appendix D, p. 670.

In addition to size range the following chart shows the longest claws attained within each group.

Distribution of Size in the Genus Uca *(mm)*

(As Indicated by Lengths of the Largest Known Individuals in Each Species)

Size-group	*Carapace lengths*	*Propodus lengths*	*No. of Species**	*Subgenera represented*
Gigantic	30-33	87-109	3	*Afruca, Uca*
Very large	25-29	66-80	3	*Deltuca, Uca*
Large	20-24	50-71	10	*Deltuca, Uca, Minuca*
Moderate	15-19	31-58	11	All except *Afruca* and *Celuca*
Small	10-14	22-53	22	All except *Boboruca, Afruca,* and *Uca*
Very small	5-9	10-24	22	*Australuca, Amphiuca, Minuca,* and *Celuca*

*Sometimes represented, through subspecies, in two size-groups.

In the systematic section a few sample measurements follow the morphological description of each species. These are intended merely as guidelines to future investigators, showing the largest specimens that have been on hand, or those of unquestioned identity appearing in past publications; these figures are the bases of the chart above. Also included in the systematic section are measurements of moderate-sized males that are more typical of most specimens to be encountered in the field and in collections. These measurements, in combination, of the largest and intermediate males, also give a preliminary indication of the allometric curve when the ratio of carapace length to propodus length is compared at these two points.

In his classic paper on allometry in *Uca p. pugnax* and in *minax*, Huxley (1924) remarked that in groups characterized by such continuing allometric growth the usual bases for morphological species designations were useless since the individual had no fixed form. He suggested that in such cases the k values, which indicate the rates of proportional growth in various pairs of characters, might prove to be important specific distinctions.

This ratio, whether based on measurements or, as in Huxley's study, on weight, proves to be of little or no value for taxonomic purposes in *Uca*. First, there are so many species of similar size and proportions that their differential growth ratios in many instances coincide. Second, and far more interesting, adult proportions are attained at different lengths in different populations of the same species. Just one example, that of a group of (*Minuca*) *rapax* populations, is given here (Table 11). I have found similar differences in two populations of (*Celuca*) *lactea annulipes* taken in different biotopes on the island of Zanzibar, as well as of *lactea perplexa* on the northwest side of Viti Levu, Fiji. One of the groups of *lactea* lived farther upstream than usual, while the other occupied a normal habitat near mangroves. Again, because of the different proportions of leptochelous and brachychelous individuals, k values can differ in accordance with the prevailing claw form of the invariably few individuals of large size. The difference can be striking in Indo-Pacific subgenera where extremes of the two forms occur in almost every population. Samples of adequate size would, of course, take care of the difficulty. Finally, when comparisons of claw size to crab size are made by weight, variations exist in degree of tissue shrinkage, size of air spaces, and amount of liquid; these differences depend only partly on whether freshly dead or preserved crabs are selected for the work; it seems preferable, therefore, to use carapace length in relation to length of propodus (manus and pollex) rather than weight of crab in relation to weight of claw.

In every species of *Uca* the propodus attains a length of at least twice the length of the carapace. Both fingers of the chela—the pollex portion of the propodus and the opposing dactyl—also elongate allometrically with respect to the manus. The extreme of both forms of elongation is reached in (*Celuca*) *festae*; in one individual the longest propodus measures 4 times the carapace length, while the dactyl is almost 7 times the length of the manus.

Early in the study a practical rule was needed to determine the size at which an individual male should be considered mature, whether alive or preserved. The indication used has been the dactyl's length; when it is clearly longer than the manus the crab is considered mature; except in a very few species, such as *latimanus*, all characterized by paedomorphic claws, the gauge seems to work. By the time the dactyl has surpassed the manus the specific characteristics of armature and gonopods are well developed, and individuals with shorter fingers only rarely display and court.

During growth the major merus also increases allometrically in direct relation to the similar growth of the propodus and dactyl, all of which of course are functionally closely related. In addition, the breadth of the carapace especially anteriorly increases with size, the degree differing with the species. Further changes in proportion are mentioned later in this chapter in connection with individual structures. It seems likely that the proportions of the rare giants in each species illustrate size limitations imposed by sheer weight.

Altevogt (1955.1, 1955.2) recorded in India the total weights and weights of the major chelipeds in a series of *vocans*. His largest specimen, weighing 7.40 gms, carried a cheliped of 3.56 gms—more than 48 percent of its total weight. In a series of *maracoani* we weighed in Trinidad, the heaviest claw proved to be slightly more than 40 percent of the crab's total weight, its live weight being 8.09 gms and the weight of the autotomized cheliped 3.32 gms. Although in both species these proportions are rare exceptions, maximum weights of about one third of the total weight are common in species both large and small distributed widely throughout the genus. Males within the normal size range of socially active adults perhaps usually carry chelipeds weighing a quarter or more of their total weights. Comparative series of weights, made on representative species in the various subgenera and using samples of adequate size, would prove of interest.

Female *Uca* are almost always smaller in their carapace dimensions than the largest known conspecific males, and as a rule smaller also than many of the displaying males in the actively breeding part of a population. Females less than two-thirds the maximum female size known in a species sometimes carry eggs, the abdomen being apparently always of adult breadth before they do so. Small, immature females are occasionally courted vigorously by mature males, usually with herding (p. 503), and small males with major chelipeds of juvenile proportions sometimes try to mate, apparently without success (p. 121).

Biologists wishing to inaugurate studies on fiddler allometry will find useful discussions and references in Huxley, 1924; Huxley & Callow, 1933; Gray & Newcombe, 1938.1, 1938.2; MacKay, 1943; Gould, 1966; Herrnkind, 1968.2; and Mayr, 1969. In the present study the following figures illustrate allometric growth in various structures: 24, 25, 27, 30, 35, 37, 45, 47, and 48.

The subject of regeneration properly belongs in the realm of physiology and so will be excluded here except for two statements that still appear to be needed, judging by continuing verbal enquiries and recent non-technical publications. First, when a major cheliped is autotomized the regenerated major cheliped always grows on the same side of the crab on which it was previously located; second, when differentiation begins, at or soon after the second post-megalopal stage, it does not result from the loss of a cheliped. Incidentally minor chelipeds in males and either cheliped in females are only rarely lost at any age. These points have been established by Vernberg & Costlow (1966), by Feest (1969) and by me (unpublished).

Large claws occur about equally often on the right and left. As examples, in populations of *tangeri*, *rapax*, and *lactea* 50 males of each were checked.

D. General Shape

When viewed from above, the carapace ranges from almost quadrilateral to clearly hexagonal. The differences depend on the width of the front, the degree of the backward slant of the orbits, and the convergence of the sides as they approach the posterior border. In most species the orbits of adults are so slightly oblique and the sides so little convergent that the crabs seem almost rectangular; the breadth is always a little greater than the length. Females usually have both the orbits and sides slightly less slanting than do males.

The orbits of young crabs always slant more than do those of adults, sometimes strikingly so. Nevertheless, species having more horizontal orbits as adults show this tendency, in comparison with slanted species, from the early post-megalopal stages. (Figs. 1, 24.)

The paedomorphic carapace shape is marked in only a few species. In the Indo-Pacific these include *rosea* and *triangularis*, and, in the Americas, *pygmaea* and *zacae*. The shape is not apparently associated with paedomorphism in other characters, such as the size, proportions, or armament of the major cheliped.

Slanting orbits are associated in both young and old with dorso-lateral carapace margins that converge strongly posteriorly. To a lesser extent the vertical lateral margins also converge most in forms with slanting orbits. Another feature of the carapace associated with scarcely oblique orbits and sides is the presence of distinct, antero-lateral margins, converging little or not at all, or even diverging, before they turn to continue as the dorso-lateral margins. Sometimes, as in the subgenus *Minuca*, the antero-laterals are extensive. In other examples, as in (*Deltuca*) *dussumieri*, they are rudimentary and individually variable. Throughout the genus they vary even on the two sides of the same individual, especially in males, where they tend to be longer on the side of the major cheliped. In most species they are less developed in the young than in adults; an exception is (*Celuca*) *stenodactylus* (Fig. 24 *K*, *L*, *M*).

In adults, throughout the genus, the carapace is wider than long, the length being roughly 60 percent of the width. In young crabs the breadth is always relatively less than in adults.

The regions of the carapace are poorly marked, especially in a few species that are periodically subject to desiccation. Here the hepatic and branchial regions are often altogether fused and project well above the general level of the carapace, which in the same species is also exceptionally arched (Fig. 25). The difference between *rosea*, one of the least arched, and *stenodactylus*, one of the most curving, is considerable even in the smallest crab stages.

The same figure shows the difference in orbital slant, and the correlated ventral curvature of the sternum and abdomen.

The aspects of the carapace so far considered are degree of orbital slant, presence of antero-lateral margins, degree of lateral convergence, relation of breadth to length, projection of hepatic and branchial regions, and degree of arching of the carapace as a whole.

All of these characteristics increase the crab's volume, particularly that of the empty space covered by the hepato-branchial regions. They seem obviously to be associated with a single ecological adaptation, the avoidance of drying out. Not one of the traits varies oppositely from the others. For example, a crab with strongly slanting orbits and strongly converging lateral margins never has long antero-lateral margins, a high-arched carapace, or projecting hepato-branchial regions.

These occasional needs to conserve moisture fit in well with the variations in carapace characteristics both among the species and in post-megalopal development. For example, all young crabs, being both small and equipped with slanting orbits, tend to live closer to low-tide levels than do adults, and accordingly are less subject to desiccation. Similarly, all species having strongly slanting orbits as adults live in habitats normally moist and partly shady.

In contrast, whenever the shape of a species results in an unusually large volume, its members always prove to be exposed at times to risks of drying out. The hazards may occur in at least one of four ways. First, during a tropical dry season any burrows above normal tidal levels may be dry for weeks, except, no doubt, for periodic subsurface moistening by spring tides; during these weeks or even months the crabs do not emerge at all. Second, some crabs burrow on flats always dried out during the neap tides, and are only active during the fortnightly spring periods; how much risk of desiccation they run at the bottom of their burrows is still unknown; the fact is that these species always show a large volume for their size.

Third, several species hibernate in the frozen mud of nearly freshwater swamps and river mouths. Finally, a number of very small, tropical species display for long periods in blazing sun, without moistening their gills in the water at the bottoms of their burrows.

Good examples of highly arched species that aestivate seasonally, during neap tide periods, or both are some populations of *galapagensis* in the eastern Pacific and *inversa* around the shores of the Indian Ocean. Both *arcuata* in Japan and *minax* in the northeastern United States regularly hibernate in those parts of their ranges and are notably arched. Since the larger specimens always live in almost fresh water, their burrows are probably often frozen solidly in winter. It is notable that *pugnax*, a species broadly sympatric with *minax*, is not shaped in such a way that it attains maximum volume for its size, and it is always smaller than *minax*; expectably, it lives in more saline marshes where tides probably reach the bottoms of hibernation burrows even during prolonged periods of surface freezing. A comparative study of the ecology and physiology of aestivation and hibernation in these species would be most interesting.

U. saltitanta, a very small species in the eastern Pacific, will serve as a good example of a form that displays with prolonged vigor and shows all the features resulting in a large volume. Its range is strictly tropical and its burrows always close to low-tide levels, so that neither seasonal nor semi-lunar desiccation could ever be threats. Yet its preferred substrate is always dark mud in open sunlight, while its peak display periods extend through the noonday heat, all characteristics promoting maximum temperatures at the time of their greatest activity. Yet *saltitanta* displays as vigorously as any known species, and for astonishingly long sessions. One individual continued for 20 minutes. Its endurance must be aided not only by its shape but by its brilliant white display color.

Several other American species, *stenodactylus*, *leptodactyla*, and *latimanus*, not only are very small and yet display in baking sun for many minutes at a time, but also often have burrows subject fortnightly to desiccation during neap tides. Their large volumes must, it seems, be doubly useful.

E. FRONT

The front of the carapace is not associated with the adaptation to avoid desiccation. This tongue extends ventrally between the eyes (Figs. 1, 26) and varies in width from less than a fifteenth to about two-fifths the width of the carapace. The front's breadth and shape are similar within subgenera, but there is often marked individual variation, and females are as a rule slightly wider than males. Both the narrowest and broadest examples (subgenera *Uca* and *Minuca*) are American. A shallow, central furrow usually is evident, as is a low rim continuous with the orbit's dorsal margin. This rim is almost always broad and smooth, but very rarely is minutely beaded on one or both edges.

In all species except those of *Minuca*, the relative width of the front decreases during growth. In *Minuca*, however, characterized by broad fronts, the width increases relatively as well as actually. (Fig. 32.)

The adaptive values both of broad fronts and the associated shortened eyestalks remain puzzling. A narrow front obviously permits longer eyestalks and therefore makes visible more distant objects. Long stalks also serve as periscopes when a crab is feeding in shallow water (von Hagen, 1970.2). Yet some species of *Minuca*, for example *burgersi* and *rapax*, also often feed in shallow water, even though they have the shortest eyestalks in the genus, and continue to feed even when wholly submerged. Perhaps efficiency of vision has been sacrificed in *Minuca* to advantages in the morphology of the underlying nervous centers. As noted above, armature, except for the unlikely possibility of the rim, is absent; so far no appendage has been observed to rub against it.

F. DORSAL AND LATERAL ARMATURE OF CARAPACE

In addition to the equipment forming part of the orbits themselves (p. 453), the carapace bears assorted organized roughnesses that interrupt to various degrees the smoothness of its surfaces and margins. All are localized and variable, especially in males. Always, too, they are stronger and less variable in females. Only one species, the West African *tangeri*, has the dorsal carapace generally covered by large tubercles. Many species, however, are more or less finely tuberculate on the hepatic and branchial regions, especially near the antero-lateral margins. Sometimes the roughness is achieved partly or wholly by weak rugosities.

On the dorso-lateral, lateral, and posterior parts of the carapace lie a group of striae which rank with the most variable characteristics of the genus. The variability extends through all groups, among the subgenera within species, and between sexes. All of the structures, when present, are stronger in females and sometimes are only developed in that sex; all of them are sometimes altogether absent. All are formed of striae which rarely develop to the point where they may be termed ridges; they range from smooth to beaded and, rarely, strongly tuberculate. The group consists of the antero-lateral margins, postero-dorsal margins, postero-lateral striae, vertical lateral margins, and posterior margin (Figs. 1, 3).

The antero-lateral margins alone are sometimes finely serrate; usually they are minutely beaded or smooth; as described earlier (p. 451), they range from absent to moderately long. Continuing inwards and posteriorly, the dorso-lateral margins occur most typically in males as smooth or feebly beaded striae which show stronger beading in females. These striae are weak to absent and especially variable in Indo-Pacific *Deltuca* and related subgenera; contrastingly, one American species, (*Uca*) *ornata*, has them strongly tuberculate in both sexes. When present, the two postero-lateral striae lie one above the other behind and below the dorso-lateral margins. Always absent in *Deltuca*, they range through varying degrees of predictability and strength to the American *Minuca* where the upper stria is always long and strong, curves forward and laterally, and is sometimes beaded; in addition the short lower stria in *Minuca* is sometimes supplemented by similar structures, always short, which are irregularly arranged on the posterior sides. The vertical lateral margin in *Deltuca* is always weak in males, being absent at least in its upper portion. In American crabs, on the contrary, it is distinct, except uncommonly in the subgenus *Uca*, and often beaded. Behind it, continuing around the lower edge of the carapace laterally and posteriorly, usually lies a broad, smooth, raised rim similar to that of the front. It sometimes has its upper edge finely beaded, at least laterally, in continuation with the vertical lateral margin.

In spite of the variation of all these structures throughout the genus, striae, viewed as a group, are clearly weakest in Indo-Pacific narrow-fronts, particularly in *Deltuca*, and strongest in the American *Uca*, *Minuca*, and *Celuca*, where the males sometimes show as much strength in the structures as do the females. All develop gradually during growth.

Not one of these structures has yet been clearly and certainly observed in action. The nearest ap-approach to data are short motion picture scenes of several *Celuca*. In these, the meri of the middle ambulatories appear to be rubbing against either the vertical lateral margin, or the postero-lateral striae, or both; these obscure motions are in association with the definite rubbing of the ambulatories against one another in threat situations (pp. 482, 483).

G. ORBITAL REGION

1. *Introduction.* (Figs. 3, 26.) The orbits form two large sockets in the carapace opening anteriorly; within them the depressed eyestalks and eyes fit loosely. The stalk is often much more slender than the diameter of the socket, although the eye itself fits more snugly, especially in *Minuca* and *Celuca*. Throughout the genus the orbit not only furnishes obvious protection to the eye when the crab is underground, but is equipped in various fashions to drain off the muddy or sandy water that accumulates in the socket, particularly while the crab is digging. All species have a major drain at the inner, posterior corner of the orbit, where a channel passes between the base of the antennule and the end of the suborbital ridges. A second channel is always free of tubercles in the orbit's extreme outer, posterior corner. The spaces between the crenellations of the suborbital margin also provide a series of drains.

In all species, through the varied ridges, tubercles, and crenellations of its margins, the orbit forms an apparently important part of the signaling equipment of the carapace. At present we are only beginning to learn how it is used. In the following account of the orbit's divisions, this equipment will be described in more detail.

2. *Eyebrow.* The eyebrow, a curving, double-bordered section of the dorsal edge of the orbit, lies immediately above the central part of the depressed eyestalk. It ranges from almost non-existent in Indo-Pacific narrow-fronts to wider than the stalk's thickness in some *Celuca* (Fig. 26). It varies similarly in its degree of verticality; sometimes it is completely visible in a dorsal view of the crab and sometimes it can scarcely be seen except from the front. Its proximal and distal borders are uncommonly marked by smooth striae, but usually by finely beaded edges, of which one or the other is often much the stronger throughout related groups of species. The eyebrow and its beading are well developed in young crabs. Its function at any age is unknown.

3. *Antero-lateral Angle.* This fixed point on the carapace ranges from bluntly obtuse to acutely produced; its shape on two sides of the same male and even female are often somewhat different; in males the more produced angle is on the side of the major cheliped. The angle's sides and the adjacent anterior and lateral margins of the carapace are sometimes minutely serrate or tuberculate as is, rarely, the ventral margin of the angle. There is little change with growth, except that in wide-angled species the angle is more acute in small crabs, while in all species any inequality on the two sides increases with age. In at least several species the angle is rubbed by at least the major merus in threat situations; details are not yet known.

4. *Suborbital Margin.* In most Indo-Pacific *Uca*, the antero-ventral margin of the eye is almost entire, with low crenellations confined to the outer half of the lower margin of the orbit. Toward the middle or inner part of the orbit's floor, these crabs often have either a distinct ridge or mound, or else there is a row of tubercles, which varies considerably within species and is sometimes found only in females.

These tubercles occur in males in some *Deltuca*, in *Australuca*, and in the west African *tangeri* (*Afruca*); very rarely they occur in female *Celuca*. In all species with weak crenellations but with prominences, tubercles, or granules on the orbit's floor, the general aspect of this part of the orbit is rolled out.

In contrast, species of *Thalassuca* and *Amphiuca* in the Indo-Pacific, the West African *tangeri*, and almost all American forms have well-developed crenellations extending the full width of the lower orbit and sometimes continuing along its outer margin. In every species the crenellations are accentuated close to the margin's antero-external angle. Often they are simply larger than elsewhere; sometimes they are distally truncate and directed strongly outward; sometimes a series is fused into a strong, projecting ridge; often the spaces between them are wider and more deeply incised. Throughout the genus, weak crenellations are often associated with profuse setae and, sometimes, pile, both on the floor of the orbit and on the suborbital and pterygostomian regions. Often only the crenellations of the outer angle are unobscured.

Without exception, species that live on sandier rather than muddier shores have stronger crenellations, fewer setae, and less pile. Except in many *Celuca*, which are often notable for strong crenellations in both sexes, this marginal equipment is usually stronger in females than in males and they sometimes have less pile around the crenellations.

Our knowledge of the functions of the crenellations is rudimentary. It is certain, both from field observations and from motion pictures, that at least the crenellations of the outer angles are sometimes rubbed by the dorsal and postero-dorsal armature of the major merus in males; at least in some *Celuca*, the action of the merus is probably best described as a vibratory tapping, rather than as a rub. It occurs in threat situations and, perhaps, in some unmixed courtship displays. In addition we know that the minor cheliped in males and both chelipeds in females rub against the crenellations. In no single case are the exact juxtapositions of segments and their parts clearly established (p. 482).

5. *Suborbital and Pterygostomian Regions.* These areas, immediately below the orbits and each other, may for convenience be briefly considered along with the orbits. Functionally they have perhaps more in common with the third maxillipeds which lie between them, since their pile and setae, profuse or sparse, apparently play a role in the aeration of water recirculated through the gills, the associated cooling of the body (Altevogt, 1969.2), and on occasion of the eggs (p. 472).

In all species the region immediately below the lower orbital margin is somewhat flattened and bordered posteriorly by a sinuous ridge; in general it is concave anteriorly and stops short of the orbit's inner corner; it apparently forms part of the system draining muddy water from the orbits. The surface of the suborbital region is usually more nearly naked than is the pterygostomian area, which is always well provided at least with short, sparse setae; these setae extend laterally to the vertical lateral margin, where they abruptly cease. In general the suborbital and pterygostomian regions are similarly equipped in any given species, being in some setose and relatively flat, and in others nearly naked and strongly convex; often the pterygostomian region is tuberculate. Since the roughness is frequently completely concealed by setae, it does not seem likely that the tubercles can then function in any form of sound production; our ignorance of the subject, however, remains complete. As with the dorsal part of the carapace and the third maxillipeds, mud-dwellers show less convexity than do species living in sandier habitats.

6. *Growth of Orbital Structures.* In young *Uca* the orbits are relatively deeper dorso-ventrally than in adults, in correlation with the wider eyestalks. Eyebrows are narrow or absent in the youngest crabs. Prominences, granules, or tubercles are discernible on the orbit's floor, when characteristic of a species, in the youngest post-megalopal individuals; sometimes, as in *dussumieri* (*Deltuca*), prominences are better developed in young crabs than in adults, although this is not true of granules and tubercles. Marginal crenellations are always weak or undeveloped in the smallest crabs. The characteristics of the suborbital and pterygostomian regions develop gradually. (Fig. 27.)

H. ANTERIOR APPENDAGES

1. *Antennae and Antennules.* These organs are small and inactive in *Uca*, in comparison with their size and importance in aquatic forms. Comparative counts of the segments of the antennal flagellum have not been undertaken, except for a token examination of three widely separated species, *dussumieri*, *maracoani*, and *minax*. In each of these forms, the segments in three males numbered between 30 and 40.

In common with other crabs, *Uca* has no statocysts and there is at present no evidence that the antennules play any part in the detection of vibrations. At least when a fiddler crab is on the surface, they are kept folded in their sockets below and behind the front (Figs. 26, 28); they never show overt motion when in the presence of possible airborne chemical stimuli, as during courtship. In short, at present any comment on the functions of these organs simply underscores ignorance.

2. *Eyes and Eyestalks.* As will be seen from Figs. 31 and 32, the length and relative thickness of the eyestalk and the size of the terminal eyes are exceedingly

variable throughout the genus. The species with the longest stalks are members of the Indo-Pacific subgenus *Deltuca* and the American subgenus *Uca*; all of the longest stalks are also the most slender, lying loosely in the orbits. In broad-fronted crabs the stalks are of course shorter, since in these species the carapaces are not correspondingly wider. In short-stalked forms the stalks are also relatively thicker. Crabs with slender stalks usually have the diameter of the eye greater than that of the stalk; especially in the superspecies *coarctata*, the eye is notably bulbous (Fig. 31 *A*). In contrast, in very broad-fronted crabs (Fig. 31 *H*) the eye projects scarcely at all beyond the circumference of the stalk. In a few species (Fig. 31 *E*) the depressed eye projects distinctly beyond the presumably protective antero-lateral margin of the orbit; these crabs do not live in the mud.

In several species of *Uca* the eyestalk and orbit on the major side are considerably longer than those on the minor, growing allometrically. The best examples, both in the subgenus *Uca*, are *maracoani* and *ornata*.

In two related species, *heteropleura* and *stylifera*, the eye on the major side in adult males is sometimes equipped with a terminal style of variable length, similar to those found in some species of *Ocypode*. In almost all species of the same subgenus, *Uca*, the style occurs in some young males but not in adults. The structure is never strikingly colored to human eyes, even when the crab has attained the polished white of display coloration; it seems to be too slender to add to the crab's conspicuousness. It plays no part in waving display or advanced courtship. Work on possible endocrine involvement has not been undertaken. In short, the style's function remains unknown. Von Hagen (1970.2) has recently reviewed the problem.

The young of all species, whether Indo-Pacific or American, have the eyestalk relatively thicker, with the eye larger, than do adults (Fig. 32). As the front is proportionately wider in young than adults in all subgenera except *Minuca*, so the eyestalks are shorter in the young with the same exception. In other words, almost all species in *Minuca*, both in the shape of the front and length of the eyestalks, accentuate the post-megalopal characters of the genus, in a distinct form of paedomorphism. In very young *Uca* the eyes in the rest position tend to project beyond the antero-lateral angles, as is usual in megalopa.

3. *Maxillipeds and Other Mouthparts.* As in other crabs, the maxillipeds are concerned with the ingestion of food and involved in the respiratory system. In addition, the flagellum of the third maxilliped is one of the appendages used in cleaning the eye. Fig. 33 shows the structure of the three pairs of maxillipeds, in comparison with those of *Ocypode*, the other genus considered to be in the same subfamily; see also Figs. 76, 77 and 78. Comparison may also be made with the mouthparts of *Cancer*, figured in Pearson's monograph (1907-1908). The most notable specializations in *Uca* are the development of spoon-tipped setae on the second maxilliped and of the gill on the third. The gill will be discussed along with the gill system (p. 469).

Both the sculpturing and patterns of external setae on the third maxillipeds are basically similar throughout the group and in detail they have not proved very helpful as taxonomic characters. Channeling, probably as part of the external drainage system, is notable in species of *Minuca*, most of which live in mud or sandy mud rather than in muddy sand. In species of *Celuca* with strongly arched carapaces and sterna, the ischium and merus of this outermost maxilliped are also unusually convex. In *Minuca*, the merus of the third maxilliped is relatively large in respect to the length of the ischium. This can be viewed as a minor paedomorphic character, since the merus throughout the genus is slightly reduced in relative size during growth.

On the second maxilliped the inner edge of the anterior half of the merus, along with the tip of the palp, usually has some setae ending in concave, pectinate expansions; these are here termed "spoon-tipped setae." In some species they are almost lacking, while in others they may total several hundred individuals, arranged in numerous rows and covering more than half the inner surface of the entire length of the maxilliped. Examination of a majority of species in the genus has shown that those species living primarily on muddy substrates have few spoon-tipped setae, while those in environments most nearly approaching sand have the most. Examples of the various forms occurring are given in Figs. 36 and 37. The question of ranges of variation among different populations living on somewhat different substrates has not been investigated. It is not yet known whether the number of scallops on the spoon vary in accordance with habitat. One characteristic of probable phylogenetic importance is the proximal, spine-like protuberance found only in *tangeri* from West Africa and in all six members of the American subgenus *Uca*. (Fig. 37, *E*, *F*, *G*.) Spoon-tipped setae appear early in the life of the crab, but do not reach their final numbers until the individual approaches maturity.

Uca's method of feeding appears simple. To casual observation the crabs seem literally to be eating mud. At low tide a fiddler scrapes up pinch after pinch of substrate with a small cheliped and thrusts the pellet into the buccal region. Here, however, the inner maxillipeds function together in a complex straining procedure that separates edible matter from most of the inorganic particles. The organic portion, still slightly mixed with substrate, then passes into the stomach, while mineral matter is rejected. Because of the activities of the mouthparts fiddler crabs are usually called filter feeders.

The first account of *Uca* which attempted analysis of both food and method was that of Verwey (1930). Crane (1941) described the spoon-tipped setae and suggested their association with muddy or sandy habitats. Altevogt (1955.1, 1955.2, 1956.1) carried analysis and description much farther, including an account of the process by which edible particles are floated away from the heavy inorganic matter. Finally, Miller (1961) described the functions of the many appendages and their parts involved in the complex process, contributing new facts and probabilities. He also presented additional ecological evidence for the differences observed among the mouthparts of three species. More recently, Ono (1965) provided data on *Uca lactea* in Japan.

The following summary of the role of the inner maxillipeds and other normally concealed mouthparts is taken essentially from Miller. A general account of feeding, as a major behavior pattern, starts on p. 472.

The rapid and complex motions in the buccal cavity are unfortunately wholly invisible under natural conditions. A good idea of them may, however, be obtained by removing the third maxillipeds, placing a bit of substrate on the exposed inner mouthparts, and observing the subsequent activity through a dissecting microscope. The ingested particles consist principally of light-weight edible matter and coarser inorganic particles. All are trapped in the long setae of the first maxillipeds. Against these the matted setae of the second maxillipeds now press. The area is simultaneously flooded by water from the branchial chambers. The second maxillipeds in vibrating, lateral sweeps free the coarser particles from the first maxilliped, catching them between specialized setae, including those with spooned tips; during the sweeping motion these and other setae scour the particles free of filmy food material, which is left caught in the setae of the first maxillipeds.

From there the comb-like setae of the vibrating maxillae pass the material backward, probably removing further inorganic matter. Finally it is drawn, still somewhat mixed with mineral substrate, between the mandibles.

Meanwhile, when the second maxillipeds reach the lateral ends of their rapid sweeps, they break away from their closely appressed, scouring position against the first maxillipeds. At this instant the heavy inorganic particles are washed down and back to the base of the buccal cavity.

Here, when an intact crab feeds normally, a wet gobbet appears and grows rapidly in size. Usually a small cheliped wipes it off, after every few clawsful of substrate, and drops it on the ground as a pellet; sometimes it falls off of its own accumulating weight.

I. MAJOR CHELIPED

1. *Introduction.* Nothing approaching the exaggeration of this appendage is found in other crustaceans, even among lobsters. For comparisons in the animal kingdom one must hunt far; deep-sea Gulper Eels (*Eurypharynx*) with their elongate jaws are the best examples that come to mind. Antler-bearing mammals, including even moose and Irish elk, show in contrast minor specializations. In fiddler crabs the claw alone, at its maximum relative weight, reaches almost half the total weight of the crab. In length, the same part of the fiddler sometimes measures more than three times the length of the carapace. At its extreme, the claw attains four times the carapace length and, in the same species, the major dactyl seven times the length of the manus.

The segments divide functionally into three groups (Figs. 1 and 2). First and most proximal are the basis and ischium; the merus and carpus form the second pair; finally, the segments of the claw itself form the third group, composed of the propodus (manus and pollex) and the dactyl. As in other decapods, the pollex is a fixed extension of the lower distal part of the manus; attached to the latter's upper distal end is the dactyl or movable finger. The dactyl and pollex together are termed the chela, with prehensile edges formed by the upper margin of the pollex and the lower of the dactyl.

The basis and ischium, while important in the movement of the merus and hence of the entire appendage, are small, relatively invariable, and unarmed, except for occasional granules or spinules which are always minute and variable and have never been observed in use. These two proximal segments will not be considered further.

In addition to their muscular functions during display and combat, the merus and carpus both are equipped with a variety of structures apparently used only in threat, or possibly in courtship situations, and never in combat. At these times, roughnesses on the merus are rubbed or rapidly tapped against correlated structures on the anterior and antero-lateral parts of the crab's own carapace, or against the merus of an ambulatory. Sound is undoubtedly usually produced by these motions, but the recorded evidence is still scanty.

Finally, the claw itself is used principally in waving display, where it is rhythmically moved, and in combat with other males. Additional uses occur in sound production, when it sometimes vibrates against the ground in both threat and courtship. In a few species, certain tubercles apparently also signal by rubbing against an ambulatory. When viewed as a whole, the appendage shows a striking functional dichotomy. The armature of the merus is self-directed, chiefly against correlated structures on the carapace. That of the claw, with rare exceptions, is directed toward particular structures on the claw of another individual. Yet, regardless of additional minor uses in the acoustics of courtship, the entire complex armature of both merus and claw forms a vast system reserved for intermale behavior.

2. *Merus and Carpus.* These segments are larger or smaller in conformity with the allometric growth of the manus, pollex, and dactyl. The result is that the tip of the chela always, in the folded rest position, lies either directly in front of the buccal region or somewhat beyond it, on the side of the minor cheliped.

With a few exceptions, the merus is a stout segment. It is always convex and partly roughened posteriorly and dorso-distally. Dorso-proximally and anteriorly it is flat and almost always smooth. Details of the range of its armature are given in the taxonomic description of the genus (p. 15). Table 12 gives the known instances of the armature's use.

This armature is almost always strongest along the antero-dorsal margin, particularly at its distal end where adjacent tubercles also often occur in the upper distal end of the anterior surface. In young crabs this distal complex can come into rubbing or vibratory contact with the crenellations of the outer suborbital margin. In larger individuals, however, allometric growth puts the segment's end altogether out of reach of the carapace. Perhaps any stridulatory or vibratory function this area may have is important only in juveniles, since in mature males waving display may supplant certain acoustical threats.

The postero-dorsal margin in most subgenera is strongly angled only in its proximal part and throughout is scarcely armed; distally it tends to obsolescence and is sometimes absent. On each side of this distal marginal area, the dorsal and posterior surfaces are more or less roughened. Even in the many species where these regions are nearly smooth, some rugosities persist dorso-posteriorly near the segment's distal end. This area, at least, seems sometimes in young crabs to vibrate against the suborbital region, the antero-lateral angle, or both. As with the antero-distal tubercles of the dorsal margin, allometric growth carries these rugosities beyond the possibility of such contact. More proximal and posterior rugosities apparently serve the larger crabs, and even the postero-distal armature is for them within reach of at least the first ambulatory.

The smooth, proximal section of the dorsal aspect of the merus comes most easily into contact with the adjacent outer pterygostomian region; such contact would seem, from a signaling point of view, to be ineffective, since the region is always setose. The fact that this part of the carapace, like the entire antero-dorsal and lateral areas, covers chiefly empty space should, however, be kept in mind; it may well prove true that some of the vibratory motions of the merus consist only of tapping this smooth portion against the pterygostomian region; preliminary observations and films give some support to this notion. Perhaps the underlying airspace provides a drum-like resonating chamber. This structure might also reinforce the more conventional forms of stridulation suspected to result from the frication of some of the meral armature against the suborbital, antero-lateral, and lateral structures of the carapace.

Rubbing also certainly takes place against the dorsal meral margins of at least the more anterior ambulatories. Which merus in the latter contacts does the rubbing is not yet clear, but it seems that both the cheliped and the leg may at times be active.

Distally and subdistally the dorsal part of the merus shows two parallel ridges which are usually armed with minute tubercles or serrations. Their use is unknown.

The third margin, the ventral, is always sharply angled and more or less regularly equipped with small tubercles or serrations. Its function, again, is unknown.

The carpus, usually almost as broad as long, like the merus is anteriorly flat and essentially smooth, while it is rounded and usually rough posteriorly. Dorsal flattening is characteristic, in conformity to the dorsal part of the carpal cavity of the manus, into which it fits when the cheliped is flexed at rest. The dorsal and posterior armature ranges from rugose to tuberculate and is sometimes almost lacking. The dorsal margin, the ventral, and a low, oblique ridge on the anterior surface usually have a few tubercles, always very small except for rare enlargement on the anterior ridge. None of them has been observed in use; they do not seem suitably located for stridulation in conjunction with any part of the adjacent inner manus (palm).

3. *Manus, Pollex, and Dactyl.* This section, the claw, forms a functional whole which may be viewed in several ways. It attracts an observer's attention first in waving display; here its large size, rhythmic motions, and often striking colors all make it conspicuous. It also acts as a grasping organ, whether the object seized by its prehensile edges is another claw or a human finger. Finally, it is one of the most highly and variously specialized organs known to zoology, and certainly is unsurpassed in the number of adaptations for ritualized combat. The emphasis in this section will be on the last aspect.

The variety of armature on the claw appears at first bewildering, even when the basic functions of the structures have become apparent. A count of distinct structures on the claw of a single subgenus, *Celuca*, totals 84 (Figs. 42, 43, 44; Table 13); each of these may be justly considered a unit, it seems, since each on occasion varies independently of its neighbors. The table also indicates the range of variation within each unit. Of these 84 structures, about 60 are known to be used in at least one combat component in at least one species of *Celuca* or the related genus, *Minuca*. Each of the two species in which the forms of combat are now most familiar employ more than 40 of these structures in their combat repertories (Table 14). The particular structures used in a given combat depend not only on the forms of the combat components employed, but also on whether the combat is between homoclawed or heteroclawed individuals, on notable differences in size, and even on whether the first actor approaches his opponent from the outer side of the latter's manus or from the palm side.

The structures as a whole are arranged in orderly groups, regardless of their wide range of variations. They divide in general into ridges, mounds, grooves, pits, depressions, and associations of tubercles; almost all are highly localized and usually of limited variability within species.

Only the outer side of the manus is relatively homogeneous in contour and armature, being in general convex and usually covered with tubercles. Even here the tubercles are of at least different sizes on different parts of the manus, and are often differently arranged in the upper and lower portions; often they are further specialized near a depression at the pollex base. Often the upper third or less is bent over toward the inside and more or less flattened, functionally forming a part of the dorsal margin.

In contrast, the palm has some wholly smooth areas contrasting with characteristic arrangements of tubercles, while cavities and grooves are juxtaposed with mounds and ridges. In an overall view, seven general regions are characteristic of the genus. Most proximal is the carpal cavity, a deep depression into which fits the carpus when the cheliped is folded, and the edges of which vary greatly among species in height, shape, and armature. The second characteristic structure is the oblique ridge, usually tuberculate, running approximately from the carpal cavity to the ventral margin near the pollex base. Often sharp, with a high apex beside the carpal cavity and regularly tuberculate, the ridge is sometimes low, blunt, and nearly smooth. The third major area consists of one or two roughly vertical ridges at the dactyl base, usually tuberculate; the proximal continues ventrally, rounding into the inner prehensile row of the pollex. The fourth area is the depression at the pollex base, ranging from slight to deep and smooth to deeply grooved or tuberculate. The fifth region, while less conspicuous than the preceding four and at present less well known functionally, must be of great importance, judging by the variety and complexity of its specializations. This zone is that of the dorsal margin and the adjacent submarginal region of the palm, which functionally appear closely related; a similarly close connection doubtless exists, as indicated in the preceding paragraph, between the dorsal margin and the submarginal area of the outer manus. On the upper palm the marginal and submarginal areas are equipped with various combinations of an impressive assortment of tubercles arranged in reticular and linear formations and of grooves and depressions, and often show as well notable flattenings or convexities. The sixth area, that of the center palm, varies from a distinct trough connecting the carpal cavity with the pollex depression to a convex area almost continuous with the dorsal side of the oblique ridge; finally, a proximal triangular area is bounded above by the lower edge of the carpal cavity and by the oblique ridge; it slopes from there proximo-ventrally to the ventral margin. In *Celuca* this triangular region shows a number of specializations known in one species to be used in threat, in correlation with tubercles on the first ambulatory; it is suspected of being concerned in other species in both threat and combat; these are the only structures on the claw in *Uca* known to be used in rubbing against another appendage on the same crab (p. 482). It is strongly suspected, however, that some cleaning motions made against the claw by the minor cheliped are actually stridulating activities (p. 461).

The lower margin of the manus shows a set of structures, ranging as usual independently of one another, and consisting maximally of keel, linear tubercles and, externally, an adjacent groove; sometimes they continue unbroken to the pollex tip.

Finally, the upper margins of the dactyl and the inner and outer surfaces of pollex and dactyl range from smooth to tuberculate and are sometimes grooved. The proximal outer end of the dactyl is usually tuberculate, with a submarginal groove; the tubercles often extend beyond the groove well along the dorsal margin of the dactyl. Except for this roughness, proximal tubercles usually present on the pollex, and sometimes minute tubercles near the prehensile edges, the outer surfaces of both pollex and dactyl are usually smooth; the inner surfaces are almost always so, again with the exception that minute tubercles sometimes occur near the prehensile edges.

The prehensile edges of both pollex and dactyl consistently show three rows of tubercles on each, of which the median is usually best developed and, except distally, the location of the enlarged tubercles or the rare tuberculate teeth. Any of the rows may be absent in any part of its length. Proximally the rows vary independently of the median and distal parts, and often only at their extreme proximal and distal ends are one or more rows irregular.

In general shape the chelae vary widely, as already mentioned, in length, slimness, and degree of gape. Fig. 39 gives the range of the extremes. It should be mentioned here that while *maracoani* and the related *ornata* have the broadest and most compressed chelae, other members of the subgenus *Uca*, as well as (*Thalassuca*) *vocans*, (*Afruca*) *tangeri*, and, in the pollex form only, (*Australuca*) *seismella* and (*Celuca*) *saltitanta*, are also notably deep and compressed. *U. saltitanta* is an end form, in which the beginning of pollex expansion and compression is suggested by others in the series, notably *inaequalis* and *oerstedi*.

The morphology of the claw is further complicated by the fact that each species throughout the genus tends to dimorphism of the cheliped, although the forms intergrade. In American species, the differences are much less pronounced than in the Indo-Pacific *Deltuca* and *Thalassuca*. In *vocans*, particularly, the forms are so distinct that they received variety names (*forma typica* and *var. nitida*), even though it was known at the time that both varieties occur in single populations.

Fig. 38 shows pairs of these dimorphisms in six Indo-Pacific species, and Fig. 40 in two American forms. In each case, the upper figures illustrate the heavy, high, short-fingered form with highly developed prehensile tubercles, while the lower figures are examples of individuals in the same species with the manus short and low while the fingers are slender with reduced tubercles. They will be referred to as brachychelous and leptochelous forms. Because a leptochelous chela weighs far less than an equally long brachychelous example, and because of the allometric growth of the claw, it is not surprising that the largest examples in any population often are strikingly leptochelous. It seems probable, in fact, that in the largest species, such as *urvillei*, *dussumieri*, *tangeri*, and even in American *ornata* and *maracoani*, markedly brachychelous examples eventually molt into a size making reproduction and, in time survival, unlikely, since display would be ineffective and feeding inadequate. There is evidence for this hypothesis in the subgenera *Afruca* and *Uca* (p. 512).

It should be emphasized that both leptochelous and brachychelous claws are found even among quite young crabs, on the same biotope; it seems that the differences cannot be due to differences in nourishment. Nevertheless, when chelipeds are regenerated in crabs already well grown, the result seems usually to be along leptochelous lines. Irregularities and abnormalities in tuberculation always give clues even in dubious cases to the presence of partial or complete regeneration.

The leptochelous tendency of most of the American groups is very noteworthy, and differences between the two forms in any population are relatively slight.

In development (Fig. 45), the direction of growth is from a small claw indistinguishable from the other member of the pair and resembling in all essentials the adult form of the minor cheliped. Even in the first post-megalopal instar, however, the two claws are microscopically distinct. At this stage the crab feeds with both claws, as do females throughout life, and the fingers are long in comparison with the manus (Fig. 45 *EE*, *JJ*, *MM*, *PP*, *SS*). Thereafter, with differentiation between the two chelipeds the manus and chela both grow allometrically in respect to the length of the carapace (Fig. 45 *A-D*, *F-I*, *K-L*, *N-O*, *Q-R*, *T-U*) but, in all except *latimanus*, the chela (composed of pollex and dactyl) grows at a greater rate than the manus. *U. latimanus*, therefore, in this character is strikingly paedomorphic in comparison with other species.

The armature of the pollex and dactyl develops gradually, beginning probably in the second instar, and certainly shortly after the onset of allometric growth. The proximal tuberculate ridge at the base of the dactyl and the more proximal tubercles in the gape seem always to appear very early. Young crabs, with the chela still notably short, in some species have the ventral margin of the manus tuberculate only at this time; later this armature becomes obsolescent or absent. The last major series of structures to be developed are those connected with the oblique ridge and with the dorsal margin. In large *Minuca* the tubercles and ridges of the palm tend to be reduced, apparently not through wear; in these individuals the palm may in fact lack most of its specific characters. In contrast, the prehensile edges of the chela sometimes show distinct signs of being worn down in combat. No detailed comparative study of the development of the armature has yet been undertaken; in association with a study of the development of combat, it would be sure to yield rewarding results. (See also p. 515.)

When ritualized combats between fiddlers are observed with understanding, the numerous structures involved divide into two groups. The first provides the active crab with a selection of structures used in rubbing or tapping other structures included in the second group, and located on the motionless claw of his opponent. The members of these two functional groups will be termed instruments and contact areas.

It is now clear that each area equipped with one or more of these specializations is a point of contact during the forceful pushing and grasping motion of some form of unritualized fighting. It is similarly apparent that every known component of ritualized encounters is based firmly on these varied grips. The subject will be amplified in succeeding chapters (pp. 487 and 516).

A study of Figs. 42, 43, and 44 and of Tables 13 and 14 will give a better idea of the functional relationships of combat structures than would many paragraphs of text. In ritualized combat, all of the structures on the palm are always contact areas, never instruments. The remaining zones consist of the outer manus, outer pollex, outer dactyl, lower pollex, upper dactyl, and both prehensile edges; they are all used on occasion either as instruments or as contact areas. The prehensile edges usually serve as the only instruments in high-intensity combat, while the outer parts of the manus and chela become instruments only in low intensity components, such as the manus rub.

Even in *Minuca* and *Celuca* the forms of combat are still known too incompletely to provide correlations in more than elementary or suggestive form. The following examples, based on Table 14, show the kinds of relationships that are emerging between structure and function. The components of combat mentioned are described in the glossary and in the section on patterns of combat behavior (p. 489f.).

All species in which the heel-and-ridge is a known component have in common the following three pairs of characteristics. A strongly curved dactyl is associated with a well-rounded manus heel. A moderate to wide gape is associated with a moderate to high oblique ridge on the palm. An absence of greatly enlarged teeth in either prehensile edge is associated with the contact in combat of a fairly long portion of dactyl or pollex respectively with outer manus or palm.

All species known to use the interlace have at least the proximal predactyl ridge well developed and one of several specializations resulting in a broad, smooth, median space on the proximal, prehensile edge of the pollex.

Finally, certain structures used only as areas of contact are related to other zones of similar function. The best example so far known is the outer, upper, proximal groove on the dactyl in certain *Minuca* and *Celuca*. When it is well developed, a similar groove almost always runs the full length of the outer manus just below its upper margin; the two grooves, exactly at the same level, are separated only by the junction of dactyl and manus. As far as is now known, this two-segment groove is used only as a guide for the tip of the opponent's dactyl in attaining the position for heel-and-ridging.

J. MINOR OR SMALL CHELIPED

In comparison with the corresponding appendages of most other ocypodids, the minor chelipeds are almost as specialized as the majors in general shape and size, although in the opposite direction of reduction. In every species they are far smaller than in other members of the family and, in fact, all crabs with the exception of certain spider crabs. Even in the latter examples, the entire appendage is elongated and it is only the propodus and dactyl that are strongly reduced, while in *Uca* all segments are proportionately small. Few similarities of trend can be traced between the major and minor chelipeds in any species, and often their characteristics are contrasting. For example, the minor chela in *ornata* is extremely slender, yet the major pollex and dactyl are both very deep.

The armature of the minor cheliped, while far simpler than that of the major, still varies considerably among the species. Except for the equipment of the prehensile edges, comparative study of the tubercles, ridges, grooves, and setae has not been undertaken in detail. These structures will doubtless prove to be of importance when their functions in social behavior are better known.

Like the major merus, that of the minor is typically rough on the antero-dorsal and ventral margins and on the rounded surfaces of the dorsal and posterior regions. The armature includes various combinations of serrations, tubercles, spinules, and rugosities. The anterior surface is almost always flat and smooth. The carpus often is flat above with a curved, outer, subdorsal longitudinal ridge. The lower half of the outer manus always has a longitudinal ridge at least distally that continues along the pollex, sometimes for most of its length. The dactyl often shows a faint longitudinal groove on its upper half between two low ridges; sometimes only a single ridge is present and no groove.

Minor chelipeds (Fig. 46) are notably similar in general characteristics within species groups, particularly in the width of the gape and in the relative size and character of the armature on the prehensile edges. The narrowest gapes have a series of fine serrations and are characteristic of many mud-livers, such as in Indo-Pacific *Deltuca* and American *Minuca*. Some female *Deltuca* and *Australuca* have a single enlarged tooth on both pollex and dactyl in at least one cheliped; no such enlargement is found in the male minor cheliped, except in *seismella* (*Australuca*).

At the other extreme from the narrowly gaping, serrate, minor chelipeds are the forms with wide gapes in which tubercles are absent. These are confined to species of *Celuca*, most live in muddy sand or, for *leptodactyla* and *musica terpsichores*, the substrate surface may be almost sandy, with little mud or clay admixture.

In the mud-living forms from the Indo-Pacific, plentiful setae are arranged in series both along the inside of the middle of the dactyl and pollex and marginally. In these and the species immediately following, the chelae are deeply excavate distally, forming setae-fringed spoons. In *tangeri*, as well as in *ornata* and other members of the subgenus *Uca* and in *thayeri*, two rows of subdistal setae on both pollex and dactyl form a complex "basket." This basket is highly evolved in the aberrant species *panamensis* (*Minuca*), forming a prominent tuft of stiff brown bristles.

An exceptional shape is shown by (*Celuca*) *stenodactylus* which has a well-formed basket along with chela tips that are pointed and crossed.

Finally, in the species characterized by slender chelae and wide gapes, there are few setae except for a distal basket, and the distal excavations are relatively slight.

In females, both chelipeds resemble those of the males; sometimes the appendages on the two sides differ in small details.

When post-megalopal forms are investigated, the minor chelipeds are found to be similar to those of adults except that they are relatively larger in comparison with the carapace in *rosea* and smaller in *brevifrons* and *stenodactylus* (Fig. 47). The chelae of all young crabs are less setose than those of adults, and with the onset of allometry the characteristics of the adult are rapidly acquired. The fingers show allometric growth with respect to the manus in all three of the above species, but most so in *rosea*, among the several unrelated species investigated (Fig. 48).

Although the small cheliped is used in a number of ways, its primary function is undoubtedly that of carrying food to the mouthparts. Obvious adaptations to this role are the perfectly meeting, spooned tips of the chela and the serrations of the prehensile edges, especially in mud-living crabs that must lift wet and sticky substrate. Pellets composed chiefly of sand, on the other hand, are lifted in the basket of curved setae at the tip of a widely gaping chela. *U. panamensis* scrapes algae from stones with thick tufts of stiff bristles. *U. tangeri* has a similar habit, but also lives and feeds, depending on its physiological phase, in a wide range of habitats from the wettest of low-tide mud to high on beaches of almost pure sand. Its small chela, equipped with both serrations and abundant bristles, well reflects these varied needs. After nourishment has been extracted from several pellets by the mouthparts, the small cheliped wipes away a gobbet of material that has accumulated below the posterior part of the third maxillipeds.

The minor cheliped also plucks, pats, and strokes the carapaces of courted females in all species in which precopulatory behavior has been filmed or observed in daylight above ground (p. 503).

In addition, the appendage usually makes small motions during display that roughly correspond to the movements of the major cheliped and, except in a few dubious cases, that do not at all come in contact with the carapace or other appendages.

It now appears certain that the small cheliped also acts as a sound-producing mechanism of importance. Salmon (1965) reported the rapping or knocking by a single (*Celuca*) *pugilator* female against the substrate. In addition, two other species, (*Celuca*) *deichmanni* and (*Uca*) *ornata*, were filmed during the present study; here the minor chela of a male briefly taps the ground. The behavior is shown only in a single example of each species.

More usual is the vibration or rubbing of the merus of the minor cheliped, apparently against an adjacent part of the carapace. Successful recordings have not yet been made, but films show the motions clearly in seven species, where the area of contact appears variously to be the crenellate suborbital margin, the outer orbital margin, or the antero-lateral angle. The species are (*Deltuca*) *demani*, (*Australuca*) *seismella*, (*Minuca*) *galapagensis*, and, in *Celuca*, *batuenta*, *inaequalis*, *beebei*, and *stenodactylus*. Rubbing between the minor cheliped merus and that of the first ambulatory is strongly suspected in films of (*Uca*) *heteropleura* and, in *Celuca*, of *inaequalis* and *limicola*.

In addition, it is highly probable that during some cleaning motions made by the minor, which moves toward their distal ends along the major pollex and dactyl, the crab is actually producing sound. Well suited for this are the ridges on the carpus, outer manus, and chela. Sometimes, too, the crab rubs its prehensile edges along the corresponding portions of the major. Heretofore, I have considered these motions pure displacement cleaning, when the crab was displaying with an already polished cheliped, and with evidence of a conflict situation. As in the other forms of apparent stridulation by the minor cheliped, recorded evidence of sound production has not yet been secured. Filmed examples total 23 species, distributed through every subgenus; 11 of the species are members of *Celuca*.

True cleaning by the small cheliped of another appendage can occasionally be seen, when the chela seizes the partly depressed eye itself between its prehensile edges and rubs along it, from the tip to near the base of the stalk.

K. AMBULATORIES

The walking legs are similar in form and proportions in all parts of the genus, in comparison with wide-ranging characters such as the front, eyes, chelipeds, and gonopods (Figs. 29, 30). The order of length is always the same, extending from the long second through the third and first to the short but fully functional fourth. Corresponding legs among the species differ somewhat in length but never extremely. More notable differences occur in the relative breadth of the meri and the degree of arching of its dorsal margin. In females the legs are regularly shorter and the meri wider and more arched than in males of the same species.

The armature of all legs varies more in amount and strength than in type or distribution. Most of it occurs on the merus and carpus. The merus shows a single dorsal marginal ridge, two ventral marginal ridges, and, on its posterior surface, scattered tubercles or vertical rows of tuberculate striae. These tubercles and striae are irregularly placed but are always more numerous in the segment's dorsal half than more ventrally; sometimes they occur only near the dorsal margin. The scattered tubercles occur in the Indo-Pacific subgenera *Deltuca*, *Australuca*, and *Thalassuca*; some female *Amphiuca* have both scattered tubercles and tuberculate striae; in the other subgenera all or almost all the tubercles surmount definite striae (Fig. 52). Any or all of the marginal ridges may be partly or wholly spinulous, or tuberculate, whether strongly or weakly. Often certain margins are wholly smooth and rounded, a weakness that occurs most frequently on the fourth leg; in contrast, the second and third are always more strongly equipped than the others. The posterior ventral margin always has stronger armature than the anterior, and this margin is usually stronger distally than proximally, while the opposite is true of the weaker, anterior margin. Dorsally, at the distal end of the merus, two parallel ridges, subdorsal and distal, are often equipped with minute tubercles or spinules. Variation often is found even on the two sides of the same individual.

The carpus is also importantly and variably armed. Two dorsal ridges, with or without some form of roughening, are usual on the second and third legs; the first leg usually has only a posterior ridge and the fourth only an anterior; a third longitudinal ridge sometimes occurs on the posterior surface of one or more of the first three legs, where tubercles or striae are also usual, similar to those on the merus. Like the armature of the merus, that of the carpus varies within species, and on two sides of the same individual.

Anteriorly on the first ambulatory on the major side, some male *Celuca* have minute tubercles, usually in a longitudinal row and sometimes also on the distal part of the adjacent merus and the proximal end of the manus. These special structures are correlated with the development of other equipment on the major cheliped, found on the triangular area of the lower, proximal part of the manus.

On both merus and carpus, the armature is always notably stronger in females than in males of the same species (Fig. 52).

Armature of the ambulatory mani is weak or absent in both sexes, although dorsal, lateral, and ventral ridges occur; the segment is always thinner, in the antero-posterior dimension, than the merus and carpus. The tapering dactyl is six-sided, the divisions separated by weak ridges. Both manus and dactyl are well provided with setae, often in the form of long, stiff bristles. On the more proximal segments, setae are instead usually sparse.

Pile is often importantly present on the ambulatories (p. 465).

Reference to Fig. 30 shows that the ambulatories change only in minor ways with growth. The degree of change is less than in *Ocypode* (Crane, 1937) but in the same direction of increased length. The change in length compared with carapace length is particularly evident in the growth of the merus. Again as in *Ocypode*, both merus and manus become relatively thicker. The armament develops by degrees, the legs of early instars being almost smooth.

In *Uca* the legs contrast both with those of fast-running *Ocypode* and with those of many sedentary xanthids, such as *Xanthodius sternberghii* that spends the low-tide period under stones. Although fiddler crabs are active, and sometimes exceedingly so, as in displaying *stenodactylus*, they are never racers and the moderately efficient ambulatories reflect their way of life. The most active species usually live on firmer substrates, have the longest legs, and, at least in males, more slender meri. Mud-livers tend to have shorter legs and broader meri. It is possible that slightly shorter and broader legs reduce the tendency to sink in wet mud during feeding; a wide spread of long legs would seem, however, to be more useful. If short, broad legs are useful in the mud, their frequent presence in females only may be explained. When females are carrying eggs and hence extra weight, they usually feed on soft substrate closer to low-tide levels than do males. The location would seem, nevertheless, to be more important as a means of keeping the eggs from drying out.

The following suggestions seem more likely. The shorter legs may represent the unspecialized form of the appendage; in a few male *Celuca* they have become adapted for faster motion on firmer substrates as well as for the attainment of conspicuous height in visual display. The wide meri, on the other hand, may be viewed as another adaptation in females for a more efficient expanse of stridulating surface.

The ambulatories perform an assortment of functions. All digging and the erection of chimneys, pillars, and hoods beside the burrow are performed by them, sometimes with some aid from the small cheliped. In carrying the excavated pellet, the stiff bristles of manus and dactylus form basket-like supports, regardless of any sensory functions they may prove also to have. The ambulatories often play parts in visual display, perhaps partly due to the need for balance, and also adding to the male's apparent size. Unreceptive females, in warding off males, sometimes rear high up on the tips of the middle dactyls; sometimes they proceed partly down their own burrows, leaving the ambulatories of one side extending stiffly up in the air (Fig. 89). In several species in which a curtsy forms part of display, some of the turned-under dactyls stamp on the substrate at the curtsy's low point. Salmon (1965) secured a sound record of this behavior in *pugilator*. Stamping also occurs in agonistic situations between males, especially in the subgenus *Uca*. The ambulatories also tap and stroke females in precopulatory behavior, usually in conjunction with similar motions of the minor cheliped.

The role of ambulatory armature in social behavior is certainly of great importance. In both sexes it appears to be confined to agonistic situations. Rubbing of the meri against one another occurs throughout the genus and is one of the most prevalent of social activities. It is seen even more often in females than in males; it is doubtless pertinent that their armature is always stronger than in males of the same species. The meri also certainly sometimes rub against dorso-lateral and lateral structures on the carapace, although the film evidence is still scanty. The carpi also often rub against each other and against the meri of adjacent legs.

Film analyses have shown no rubbing patterns characteristic of species or species groups. In all species photographed at some length, the meri of all four legs are shown making rubbing motions and coming clearly into contact with adjacent legs, although only rarely in the same motion picture sequence. Very often two alternate legs on the same side are used as motionless supports, while the meri of the other two are tilted so that the dorsal serrations rub against the roughness of the posterior surface of the adjacent legs. Sometimes adjacent legs, especially the second and third, are simultaneously raised, bent at the mero-carpal joint, and rubbed against each other. Sometimes the carpal ridges rub against the meri or, perhaps, each other. Often, but not always, meral rubbing occurs first on the side of the crab nearest the apparent stimulus. In all, variation and lack of stereotypy are notable in the behavior of individuals.

A quite different use of the ambulatories corresponds to ritualized combat in males. Here two females line up parallel to each other and mutually rub the extended mani and dactyls of their adjacent sides with such speed that the motion appears to be a prolonged quivering. It may be that some or all of the setae are sensory and reacting with one another. Sometimes the dactyls reach the meri of partners, and so could well be rubbing with their ridges against the marginal or posterior armature. No good photographic evidence is yet available. The females may face the same way or oppositely. Similar behavior has been observed once or twice between males and, briefly, as part of courtship. Details are still unknown.

L. ABDOMEN

The abdomen in both sexes of *Uca* has seven segments (Fig. 53 *A*, *B*). In some *Celuca* characterized by strongly arched carapaces and sterna, several of the segments are partly or wholly fused (Fig. 53, *C*, *D*).

M. GONOPOD (FIRST PLEOPOD) IN MALE

1. *Introduction.* Although the gonopods in *Uca* are usually a primary aid in the taxonomic determination of species, they must be used with care as keys to relationships and evolutionary trends. Parallelism occurs widely. Rarely the opposite tendency forms a pitfall, where a variety of shapes occurs in a single subgenus (*Uca*). Again, the gonopod of one or two subspecies in a clearly allopatric group may be aberrant. Within subspecies, gonopod characteristics are constant with minor exceptions.

A gonopod consists basically of a shaft enclosing a tubular canal and ending, in its distal one-fifth to one-sixth, in a modified tip (Fig. 56). The shaft is three-sided, its anterior, flat surface curving forward in conformity with the sternum's convexity.

The modified tip (Fig. 58) consists of the genital opening, here termed the pore, in association with a maximum of four specialized structures. Each of the four ranges independently of the others, in various parts of the genus, from absent or vestigial to extremes of hypertrophy. In this contribution, these structures are termed flanges, inner process, thumb, and setae. An additional characteristic in certain groups is a distal torsion of the shaft, along with some or all of its parts.

The basic structure of two principal forms of gonopods is shown in Figs. 74 and 75.

2. *Flanges.* These calcified wings, when present, occur on both sides of the terminal part of the canal (Fig. 58 *A*), or may extend above the pore (*B*), the canal appearing to be fastened against the postero-internal surface of the large, apparently single flange (*E*, *I*). The arrangement of simple wings on each side of the terminal pore occurs in other ocypodids, namely in *Macrophthalmus*, *Myctiris*, and *Ocypode* (Fig. 57 *C*, *A*, *D*). In *Uca* it is found in parts of the subgenera *Deltuca*, *Thalassuca*, *Uca*, and *Minuca*.

Expanded flanges, in which the end of the canal appears to be fastened directly to their continuous, convex, postero-internal side, are characteristic of (*Boboruca*) *thayeri* and (*Celuca*) *lactea*.

In the superspecies *coarctata*, flanges are progressively reduced, while the end of the tube throughout shows the antero-external edge of the tube's tip overlapping the postero-internal edge. This overlapping, with concomitant absence of flanges, occurs also in

Australuca, in (*Amphiuca*) *chlorophthalmus*, and in some species of *Celuca*. In these flangeless species, the calcified portion of the tip is often elongate (Fig. 58 *H*).

Reinforcing struts, often strongly calcified, sometimes support the flanges, and sometimes are even partially separated into spines (*dussumieri spinata*, *vocator*).

3. *Inner Process*. This structure arises at the base of the exposed terminal portion of the tube or flanges, on its inner side, toward the midline of the crab. It may take various forms, all clearly homologous; it is occasionally difficult to see, in some species because of its small size, in others because of the surrounding flesh and setae, and in still others because of its thinness and transparency. All species have it in some form, and it is clearly represented also in *Myctiris*, *Heloecius*, *Macrophthalmus*, and *Ocypode*; its occurrence in other genera apparently has not been investigated. Its three principal forms are as follows:

(*a*) A sharp, slender spine of varying extent, sometimes curved or twisted, at base of the exposed end of the tube. This spine is characteristic of the superspecies *coarctata*, the subgenus *Australuca*, and part of the subgenus *Uca*. (Fig. 58 *D*.)

(*b*) A fleshy structure, setigerous, sometimes greatly tumid and sometimes twisted anteriorly to rest against the tube and flanges at an angle. This form is found throughout *Deltuca*, except in the superspecies *coarctata*, in *Thalassuca*, in *Afruca* (*tangeri*), and in some species of *Uca* and *Minuca*. (Fig. 58 *E*, *F*.)

(*c*) A flat plate or shelf, in shape triangular, an elongate oval, or narrow throughout and distally pointed. Sometimes this process is practically fused with the tube, transparent, naked, and discernible with difficulty. This type occurs in some *Minuca*, in *Amphiuca*, and in *beebei* and related species in *Celuca*. (Fig. 58 *H*.)

4. *Thumb*. This structure is usually present, and typically almost terminal (Fig. 58 *E*, *F*). Sometimes it is strongly reduced and arises far down the shaft (Fig. 58 *B*). Rarely, it is represented only by a small shelf (Fig. 58 *H*) as in *beebei* and *stenodactylus* (*Celuca*), or is indistinguishable, as in some members of the subgenus *Uca*. Except in cases of torsion, to be described, it arises on the antero-external side of the gonopod. It is present in other genera in the family. In species where it arises well below the tip, the thumb may be highly variable even within single species in the same population (Fig. 59).

5. *Setae*. As in other structures, these vary widely in form and arrangement throughout the genus, but are distally present in profusion on every species. Because of their frequent concealment of the underlying structures, they have been omitted altogether from the drawings, except for a general view of the types in Fig. 61; here extremes of variation are shown, with examples taken from the various subgenera. It will be seen that the pattern usually includes a "mane" of rather long setae, often with certain ones isolated and elongate. In species with little or no torsion, this series is postero-external. One or more subterminal longitudinal series of setae may occur on other facets of the gonopod. Very short setae, thickly set, often spine-like and some of them curved, are found distally in most species of the subgenera *Deltuca*, *Thalasucca*, and *Uca*; they often occur on the inner process. A naked area characteristically is found antero-externally. The thumb is usually well covered with setae whenever it approaches the gonopod's tip.

6. *Torsion*. This characteristic is as notable in some groups of *Uca* as any of the structures just described.

In the untwisted gonopod, the canal proceeds up the shaft, near its antero-internal angle, until, in the terminal region, it curves externally to the pore. The specialized tip of the shaft, in conformity, is tilted externally, the inner process curving with it; one flange, termed the posterior, is directed postero-internally, the other, the anterior, extends antero-externally; the thumb arises from the anterior side of the shaft, slightly external to the path of the canal. (Fig. 58 *E*.)

In species showing torsion, on the other hand, the tip of the gonopod is twisted toward the outside (Fig. 58 *C*). Sometimes the entire tip appears slightly twisted below the base of the thumb, so that the terminal parts maintain their usual relationships toward one another, although their orientations are changed. Sometimes the torsion starts distal to the thumb, as in some species of *Minuca*, where the usual relation of thumb to inner process and flanges is changed. Torsion is most extreme in certain *Thalassuca* and *Uca*. Here the thumb may even arise postero-laterally and, continuing the direction of torsion itself, end as a strictly posterior instead of anterior structure (*vocans vocans*). In three out of six *vocans* subspecies, the canal, after proceeding in the direction of antero-external torsion, doubles back on itself terminally, to exit in something like the original position between two flanges which have themselves undergone somewhat independent torsion. In the subgenus *Uca*, torsion, along with reduction and hypertrophy of various structures, reaches such lengths that the general form of the gonopods, in five out of eight species and subspecies, is almost useless in tracing relationships.

7. *Development*. Differentiation of the gonopods starts early in post-megalopal stages; species charac-

ters, when diagnostic, are usually reliable by the time the ridging (although not the tuberculation) is well developed on the inside of the major cheliped—probably in the second or third post-megalopal instar.

8. *Function.* The invariable function of the gonopod is to pass spermatophores into the genital openings of the female. These openings, the gonopores, are described below. In no *Uca* does it seem that more than the extreme tip of the organ is inserted, although perhaps further insertion may occur in some species with elongate tips; it is apparent from comparisons that in most species it is necessary and indeed possible only for the two pores to come into contact. The fantastic variations and exaggerations found in the genus serve at most to orient the gonopod tip to the gonopore and hold it in position during spermatophore transfer; there is no trace of a complex "lock-and-key" arrangement. Gonopores are usually simple; if a tubercle is present in one position or another on its margin, manipulation shows it to be probable that the inner process on the gonopod, or a flange, or the thumb is oriented to the tubercle in a certain way. Among the subspecies of *vocans* and *lactea*, where modifications of the gonopore might be expected to occur in close correspondence to the exaggerated torsions of the gonopod, only slight adjustments have evolved, in relative sizes of tubercles and ridges; no torsion exists in the female organ. (Fig. 54.)

9. *Spermatophores.* No comparative work has been undertaken. Spermatophores usually appear in the female to be carried largely or altogether internally. In a few *Minuca*, particularly in *vocator*, they have a conspicuous external section that makes the gonopore appear more tuberculate or sculptured than is in fact the case, and can easily lead to taxonomic misidentifications. It seems likely, at least in these cases, that the protuding spermatophore prevents multiple matings. The entire subject is obviously in need of study from several points of view.

N. GONOPORE IN FEMALE

These structures are a pair of orifices on the third abdominal segments of females. Specialization ranges from a simple marginal tubercle to varying types of semi-circular ridges (Figs. 54, 64 *AA-FF*). As mentioned above, they do not show obvious torsion associated with that of their conspecific or consubspecific males. Any sculpturing does not become complete until the abdomen reaches its apparent maximum breadth with respect to its coverage of the sternum; series of measurements have not, however, been undertaken.

O. SECOND PLEOPOD IN MALE

The second pleopod in *Uca* appears unspecialized and varies little. It may serve to support the gonopod during copulation.

P. PLEOPODS IN FEMALE

As in other genera, fiddler crab eggs are attached to the pleopods, as shown in Fig. 55.

Q. PILE

Many species of *Uca* have characteristic areas of close-set, short, setae superficially resembling fur. The terms "pile," "pubescence," and "tomentum" are here considered synonymous; "pile" is perhaps preferable because of brevity. In a given species of *Uca* pile may occur on any part of the carapace, on the major cheliped, on some or all of the ambulatories, or on all of these regions. Usually it is more abundant in females than in males of the same species; an interesting exception occurs in (*Minuca*) *vocator vocator*, where pile is always present on certain lower parts of the ambulatories in males but absent in females.

Sometimes the form and distribution of pile show little variation within a species and serve as a reliable taxonomic character. Examples are eight persistent tufts on the dorsal part of the carapace in (*Celuca*) *inaequalis*, and pubescence, even more firmly attached, on the lower parts of the ambulatory carpi and mani in (*Minuca*) *mordax* of both sexes.

In most species, however, pile is both highly variable and extremely subject to abrasion. Even more irritating than this unreliability as a taxonomic character is our ignorance of its functions.

Its most obvious use is in courtship. In most or all species of *Uca*, during the final phases the male strokes, taps, or plucks at the female's carapace with the minor cheliped. Expectably the pilous areas hold mud longer than does the smooth carapace and so facilitate, and perhaps stimulate, the usually ritualized feeding motions of the male; it seems likely that the sensation of these plucking motions may be sexually stimulating at least to the female. In groups where courtship is least developed (*Deltuca* and *Thalassuca*) this behavior always precedes the above-ground mating. In groups with advanced courtship, where the crabs typically mate underground, the pattern usually takes place when the female stiffens her legs, the genus-wide signal of non-receptiveness. This occurs when the male is not fully in the mating phase or when, in unexplained instances, complete copulations take place on the surface (pp. 502-504).

In most subgenera pile occurs in at least a few species on the carapace of the female and sometimes on that of the male as well. In (*Celuca*) *cumulanta* distinctive patches are found in the females of certain populations only; in (*Celuca*) *crenulata* patches are found in one subspecies but not in the other. In two of three subspecies of (*Deltuca*) *dussumieri*, in one of two (*Deltuca*) *acuta*, and in (*Uca*) *major* the females are distinguished by a border of pile near the ventral margin of the last ambulatory merus; its function remains totally unknown.

A frequent location of pile, particularly in some *Celuca*, lies at the base of the gape in the major cheliped. As a speculation without factual support, it may be suggested that pile serves as a kind of buffer during the interlace component of combat; perhaps the pile masks noise or tactile sensations that might interfere with stimuli resulting from the rubbing of the actor's gape tubercles along the predactyl ridges of his opponent (p. 490). In general the pubescence on the major cheliped in any species is so variable and fragile that for the most part its occurrence is not specially mentioned in the systematic descriptions.

In some species, including (*Afruca*) *tangeri* and (*Uca*) *maracoani*, it seems that algae are associated with pile, especially on the propodus between the tubercles and within the pits.

In conclusion, there is no question but that pile merits close comparative study when broods of *Uca* eventually come to be routinely reared.

R. COLOR

The colors of fiddler crabs are so varied and often vivid that the only surprise is that they have not attracted more attention. Their study by zoologists has taken two main directions, which have until now remained separate. When the approaches merge we shall begin to understand the subject's intricacies, and to perceive the relations of color and color changes to ecology, physiological conditions, and behavior.

The first approach is physiological; it is concerned largely with the endogenous rhythms that control paling and darkening, and with the hormones that activate these basic color changes; the work has necessarily been confined almost entirely to the laboratory and depends on experimental procedures. The second deals with the coloration of *Uca* in the field and with their changes in association with waving display; so far this study has remained observational; the subject now invites, and urgently needs, experimental results to determine the functions of color in the genus.

Almost all color changes in *Uca* are caused by the expansion and contraction of monochromatic chromatophores, most of which are located in the epidermis. Each has permanent branching processes, so that the pigment may be either concentrated at the center, and so practically excluded from the general pattern of the crab, or dispersed into the processes. Four pigments are known in brachyurans—black or dark brown, red, yellow, and white; a fifth, blue, is found outside the chromatophores. The five apparently all occur in *Uca*; their chemistry still awaits investigation.

Fiddler crabs were among the first animals used in the study of biological clocks. During the early decades of this century the work progressed on several fronts. Observers saw that *Uca* on the northeast coast of the United States appeared darker during the day than at night. Physiologists soon found that even when they kept the crabs in total darkness the diurnal rhythm of change persisted for a long time. The investigators then discovered a similar, persistent darkening–paling rhythm that depends for its timing on the tidal schedules of the locality in which the crabs are taken. This tidal rhythm, superimposed on the diurnal rhythm, results in a semi-lunar effect, caused by the coincidence of the dark-color peaks of each rhythm and, during the same short period, the coincidence of their pale-color peaks, the effect occurring about every two weeks. At the same time that these investigations were going forward, other research showed that expansion and contraction of the chromatophores are controlled by hormones located in the sinus glands of the eyestalks and in the central nervous organs.

The contributions of Kleinholz (1942) and Brown (1944) give comprehensive surveys of the early work on the endogenous rhythms of *Uca* and their control, along with full references. For recent reviews and developments see Brown (1961) and Barnwell (1968.1, 1968.2).

The remainder of this survey of color in the genus will be devoted to the second approach to the subject—the observation of color and color changes in the field. The number of species in which color in life is known is 59 of the total of 62 species recognized in this contribution. In some our knowledge is extensive and in others scanty; only in (*Thalassuca*) *formosensis*, (*Celuca*) *helleri*, and (*Celuca*) *leptochela* have the colors never been recorded. Wherever, in the summaries given below, percentages are included, all refer only to the 59 species on which we have information.

All *Uca* change color at least to the extent, as described above, of becoming darker during the day and somewhat paler at night; the tidal rhythm induces darkening at the time of low tide and paling during high water, when the crabs are normally in their burrows. These palings are not at all similar to the temporary assumption of polished white, presumably through pigment dispersal, by some species during the display phase; instead they result principally or altogether from the simple concentration of dark pigment into the centers of the chromatophores.

All species also darken under two other conditions. When a fiddler shows display coloration as described below, it will slowly lose its polished white and any intense colors it has assumed whenever it descends into its damp burrow and remains there for more than a few minutes. No darkening effect occurs after brief stays below ground, such as are caused by alarms, short periods of digging, or descents for gill-moistening.

Fiddlers in display coloration also darken when an observer seizes and holds them. This change, in contrast to those previously described, is rapid. A released crab, even if returned promptly to its own burrow, often does not resume display coloration on the same day.

Many *Uca* change color little or not at all when in display condition. Some parts of the males, particularly of the major cheliped, are often more or less distinctively colored at all times: but the color is somewhat more intense in many displaying individuals. Other species during display show polished white to varying degrees on the carapace alone at least in some populations, while the appendages are then more or less vividly colored with yellow, orange, red, or purple. Intense blue and green are sometimes display colors, but not on the major cheliped. Finally some individuals or populations attain a polished display white that suffuses the entire surface of carapace and appendages. The following paragraphs survey the genus in regard to both general color and to color change in connection with display.

In 57 species the tips, at least, of the major chela are white or, in several forms, very pale pink or yellowish. The two with dark tips are (*Uca*) *maracoani* and (*Uca*) *ornata*.

All have some tint or shade of yellow, orange, red, or intermediate hues on the lower outer manus. This color is usually persistent except that in display phases it often becomes more intense or, unusually, suffused with polished white. Often the lower, outer manus is the only area of definite color on the crab. Where other parts of the major cheliped are similarly hued, the color in this area is the most intense. Sometimes it is so characteristic, as in (*Thalassuca*) *vocans*, that it makes a good field character.

In 12 species, roughly 20 percent, a complete color change to polished display white occurs in some individuals of some populations. Only in (*Celuca*) *l. lactea* does it seem to be the usual color of the crabs, regardless of season or display phase. In all other forms of that species, as well as in other species, its occurrence is subject to geographical differences as well as to age, sex, phase, and season. Often many individuals in a population on a particular day display and court vigorously and even successfully, attracting the attention of females and engaging in combat with other males, and yet do not assume display coloration; I have not found the converse to be true.

In 24 species, about 40 percent of the total, at least the carapace sometimes changes during the display phase to polished white (Pl. 48). Even on the carapace alone polished white has never been observed in any species of *Deltuca*, or in the two monospecific subgenera, *Afruca* and *Boboruca*. In *Australuca*, *Thalassuca*, and *Amphiuca* whitening takes place in only one species each and then rarely and usually incompletely. In the remaining subgenera—*Uca*, *Minuca*, and *Celuca*—are distributed the majority of species sometimes attaining a carapace of polished white; all these subgenera are confined to America except for two species of *Celuca*. In all subgenera, except for (*Celuca*) *l. lactea*, the full assumption of polished white even on the carapace alone is confined to fully tropical forms.

Among species in which the carapace does not become polished white, but only pales or brightens slightly if at all, several characteristics stand out.

First, only in the Indo-Pacific are found bright red and bright blue, often with white or bluish spots; here these vivid hues cover most or all of the carapace and sometimes the ambulatories as well. In American subgenera blues and greens are uncommon and confined to display coloration on the anterior part of the crab only, while red crabs in America are represented only by some populations of a single subspecies, (*Minuca*) *vocator ecuadoriensis*; their pervading hue, not connected with display, is dull rose red. In the Indo-Pacific, in contrast, certain members of *Deltuca*, *Thalassuca*, and *Amphiuca* are distinguished by the prevalence of intense reds and blues; these hues are characteristic of both sexes and persistent; they are brightest in young crabs and dullest in adult males.

Second, in a number of species of *Celuca* a marbled or mottled carapace with copper- or gold-color combined with paler or darker tones is frequent.

Third, in (*Amphiuca*) *i. inversa* and in many populations of (*Celuca*) *lactea*, particularly of *l. annulipes*, a striking pattern of transverse pale bands or marblings on a dark background is common; when display coloration is assumed, the proportions change, so that the crab eventually appears as polished white with narrow bands of dark blue or black.

Fourth, many species of *Minuca* and *Celuca* lighten somewhat when in a display phase from their usual grays, browns, and buffs. Familiar examples in the western Atlantic temperate zone are (*Minuca*) *pugnax* and (*Celuca*) *pugilator*.

Fifth, certain individuals in populations with strong display whitening go through a brief, bright stage of orange or chrome yellow that sometimes suffuses the entire crab and sometimes the carapace alone; this phase is usually succeeded by a lightening to yellowish white before polished white is assumed. I have observed these intermediate phases in certain populations of (*Thalassuca*) *vocans*, (*Uca*) *princeps*, and (*Minuca*) *galapagensis*; they probably occur in some populations of (*Celuca*) *triangularis bengali*. In each of the species the yellow phase may be the terminal one for individuals not in display phase; perhaps in *triangularis bengali* it is the terminal hue of entire populations, whether displaying or not. This suffusion of yellow occurs additionally, as far as known, only in the early crab stages of (*Deltuca*) *rosea*.

Purplish or dark red sometimes colors the ambulatories in a number of species, whether or not the carapaces whiten. Outstanding are (*Deltuca*) *demani*, (*Afruca*) *tangeri*, (*Uca*) *major*, (*Uca*) *stylifera*, and (*Minuca*) *vocator ecuadoriensis*. Bright red orange, orange red, or crimson are usual in (*Thalassuca*) *tetragonon*, (*Amphiuca*) *chlorophthalmus*, and (*Celuca*) *lactea annnulipes*.

Only one or two general statements can be made about the colors of females. In most species members of this sex are duller and often darker than the males, while individual breeding females usually assume polished display white, if they ever do so, less often than males of the same populations. Exceptions are the females of (*Thalassuca*) *vocans* and, in the subgenus *Uca*, of *major* and *stylifera*, all of which show strong display whitening in some populations. In addition, females of (*Celuca*) *l. lactea* as a whole always attain an equivalent white to that of their males. An uncommon, rose red phase occurs in individual females of *lactea annulipes* and *l. perplexa*, whether or not they are attracting courtship behavior and responding to waving males; it is also found in occasional ovigerous females of the same species; the color seems to be confined to adults.

Changes to display coloration take place gradually, usually during the hour or so before diurnal low tides. Usually they proceed to their fullest development on warm, bright days. The time needed for the change varies in different individuals within the same population, and even in the same individual on different days. The fastest such change I have seen was by individuals of (*Uca*) *stylifera*; in these the change was fully accomplished in 15 minutes or less; one of slowest was *latimanus*, which sometimes spent two hours or more effecting the change. It may be that sunlight, high temperatures, and dryness are all important. Further speculations on this topic and on the possible roles of the several pigments in effecting changes to display coloration were given in Crane (1944); none was based on experimental or analytical work and no such research seems yet to have been undertaken.

The first record of color change in *Uca* appeared as a footnote in Müller's "Facts and Arguments for Darwin," originally published in 1864. In the English translation (1869: 36) the note reads: "This smaller *Gelasimus* is also remarkable because the chamelion-like change of colour exhibited by many crabs occurs very strikingly in it. The carapace of a male which I have now before me shone with a dazzling white in its hinder parts five minutes ago when I captured it; at present it shows a dull grey tint at the same place."

A few years later Darwin continued the account: "I am informed by Fritz Müller, that in the female of a Brazilian species of Gelasimus, the whole body is of a nearly uniform greyish-brown. In the male the posterior part of the cephalo-thorax is pure white, with the anterior part of a rich green, shading into dark brown; and it is remarkable that these colours are liable to change in the course of a few minutes—the white becoming dirty grey or even black, the green 'losing much of its brilliancy.' It deserves especial notice that the males do not acquire their bright colours until they become mature. From these various considerations it seems probable that the male in this species has become gaily ornamented in order to attract or excite the female." (*Descent of Man*, ed. of 1874: 275.) Müller's own detailed account appeared in 1881 (p. 373).

Still later Alcock (1892, 1902) was of the opinion that both color and waving played roles in courtship, serving as recognition devices to the females, which also appreciated the display's color and motion. After that observers became sharply divided on the subject, as reviewed in the general account of waving display (p. 494). To this day the value of display coloration in relation to behavior remains unsettled, since even elementary experiments, save for those of von Hagen (1970.3), have not been undertaken. Its merely sporadic appearance in many species where it attains a high development is one of its most puzzling characteristics.

For experiments on the functions of color the following species would, it seems, prove to be the most rewarding, since the changes occur in many or most populations and are confined to displaying males and, sometimes, adult females: on American shores, in the subgenus *Uca*, *major* in the Atlantic and *stylifera* in the eastern Pacific; among *Celuca*, *leptodactyla* in the Atlantic and, in the eastern Pacific, *saltitanta* and *musica terpsichores*. In the Indo-Pacific no species achieves display white in most populations; in occasional places in some seasons it reaches full development in (*Thalassuca*) *vocans* and (*Celuca*) *lactea*; less often it occurs in (*Amphiuca*) *i. inversa*. Additional species that also show strong display coloration, but only sporadically, are, in the subgenus *Minuca*, in the eastern Pacific *g. galapagensis*; in *Celuca*, in the eastern Pacific, *beebei* and *latimanus*;

in the western Atlantic, *uruguayensis*; in the Indo-Pacific, *lactea annulipes* and *l. perplexa*.

Among the colored areas that appear especially promising for experimental work on their functions are the following: the lower, outer manus on the major cheliped, prominent in some threat postures throughout the genus and in vertical waves; coloration of the remainder of the cheliped, particularly when the inside differs from the outside, the two areas contrasting strikingly during lateral waving; the occurrence of contrasting colors on the anterior sides of at least the first ambulatories; further observations, in addition to experiments, on *beebei* and other species that revolve during display and that have both anterior and posterior sides of the ambulatory meri colored; the blues and greens sometimes found on the anterior parts of carapaces and adjacent areas, as in *cumulanta* and *beebei*; the large, white or blue white spots on the posterior ambulatory meri in some *Deltuca*, where they are conspicuous when raised in threat display toward the rear.

Also in need of investigation is the possibility that some of the persistently vivid colors in Indo-Pacific *Deltuca* spp., (*Thalassuca*) *tetragonon*, and (*Amphiuca*) *chlorophthalmus* may be aposematic. Similarly, while general observation shows that *Uca*, like many other crustaceans, alter their prevailing hues when not in display coloration to tone in with a variety of substrates and so achieve a kind of cryptic coloration, no precise work on the problem seems to have been effected. Finally, in spite of an occasional supposition that diurnal darkening has a cryptic value, the question has not received the benefits of experimental attention.

The course of color development in young fiddler crabs varies greatly among the species. Only among a few *Deltuca* are the very young strikingly colored; usually they appear at least as dull as non-displaying crabs in species with strong developments of display coloration. A few species have not only the tips of the two chelae but each manus as well shining white in the young of both sexes. Tones of orange or red usually appear on the major manus in otherwise dull adolescents at earlier stages than do the paler or more vivid colors of other regions of the body.

S. GILLS

The only internal structures which will be specially considered here are the gills, with emphasis on those of the third maxilliped. These gills alone show major differences and apparently have phylogenetic implications. (Figs. 76, 77, 78, 81, 82, 83.)

In Fig. 81, gills from representative species of *Macrophthalmus*, *Ocypode*, and *Uca* are drawn, using the length of the carapace as a standard. *Macrophthalmus*, which leads a life by far the least terrestrially adapted, has the best developed gills. In *Uca*, however, reduction of the anterior gills is not in conformity with the ecological requirements of the species. In any case, throughout the group these small gills at best could probably be of little use. When the gill on the third maxilliped is only a nubbin, it cannot, of course, function at all.

In no *Uca* does the third maxilliped gill approach its development in *Macrophthalmus*, or the perfection of shape in *Ocypode* (Fig. 82). *U. maracoani*, with only a few books missing from one side and orientation unchanged, is best developed; members of the subgenera *Thalassuca*, *Afruca*, and *Amphiuca* all have clearly formed books with much in common. In other subgenera, these gills show all stages of reduction. In the few species in which a long series has been examined, the character is subject to variation within populations, although some members of each will show the maximum development of the gill characteristic of the species. The species best known in this respect are *vocans*, *chlorophthalmus*, and *tangeri*.

The gill on the second maxilliped and the first regular gill, also reduced, vary among the species; either one may be the larger, with little respect to relationships shown by other characters. The species with the greatest reduction of all three small gills is *lactea annulipes*.

T. INTERNAL ORGANS

A semi-diagrammatic view of the arrangement of the internal organs is provided in Figs. 79 and 80. It is designed for only two purposes. First, for workers unfamiliar with the internal organs of crabs, it will serve as a guide in locating the gonads and determining their readiness for breeding. Second, it shows the relative positions of branchial chambers, gills, afferent branchial orifices, and pericardial sacs; some of these play not only the usual role in basic ecological adaptations but apparently also in sound production. The latter aspects will be considered in the chapter on social behavior.

A comparative study of the respiratory, digestive, and reproductive systems of representative species of *Uca*, still to be undertaken, would assuredly furnish illuminating results. Key studies based on other crustaceans including crabs are Pearson (1907-1908), Waterman, ed. (1960, 1961), and Bliss & Mantel, eds. (1968).

U. SUMMARY

The morphology of *Uca* is described, with the principal emphasis on structures that play or probably play direct roles in behavior or that are of taxonomic importance. Larval stages are omitted. The uses, known and hypothesized, of the individual structures are considered, in preparation for a discussion in later chapters of their functioning as groups in behavior patterns. Viewed as a whole, the major and minor morphological features of fiddler crabs divide into two classes—those concerned primarily with the maintenance of the animal in its environment, and those connected with social behavior. In the first group are the crab's basic shape and the equipment for respiration, feeding, and digging. In the second are the numerous specializations concerned primarily or altogether with social behavior. They include the varieties of hypertrophy in the major cheliped, the complex armature of carapace and appendages, and the diversity of gonopods. On the claw alone, comprising the manus and chela, 84 different specializations are counted that appear to function only in intermale combat. In fact, the great majority of morphological specializations for social behavior in *Uca* apparently are used only in agonistic behavior, chiefly between males, rather than in courtship. In the chapter the post-larval growth of each principal structure is briefly described and the range of variation indicated. While notable allometric growth is a characteristic of most morphological features, including its extreme expression in the major cheliped, it is not of practical use in the determination of species. Particularly in Indo-Pacific species, dimorphism of the claws is strongly apparent, although intermediate forms always occur. Color in some species varies along geographic lines and in others on the general tone of the substrate; in individuals it also depends on circadian rhythms, on breeding condition, and on whether a male is in display phase; in some species daily color change in displaying crabs is striking; even in dull species parts of the major cheliped contrast somewhat with the substrate and carapace. In practical taxonomy the most useful structures for species determination in males are unquestionably the gonopods, in combination with the shape and breadth of the front and the sculpturing of the major cheliped. Usually of secondary usefulness are the dentition and gape width of the minor cheliped, the armature of the orbits, and the shape and armature of both carapace and ambulatory meri. Of rare but important helpfulness are special armatures on the first ambulatory and the presence or distribution of pile on carapace or ambulatories. Females are distinguished from males chiefly in having two small and equal claws, similar to or identical with the minor cheliped of the male; the armature of carapace and ambulatories is invariably somewhat stronger than in the male, apparently in connection with sound production and combat, the signaling devices being more restricted than in the male through lack of a major cheliped. Taxonomically females are often difficult to determine in preserved collections from areas in which the local communities are unknown. The best key characters usually include any or all of the following: gonopore sculpturing, resemblance of front to that of male, location of pile, dentition and gape width of chela, and, used with great caution, the shape of the carapace and leg segments, all in comparison with those of their male conspecifics. In females the orbits are never more oblique than in males, the antero-lateral margins shorter, the carapace flatter, or the width of the ambulatory meri less; each of these characters always differs if at all from the expression in the male in the opposite direction, the characters together increasing the volume of the carapace and hence helping avoid desiccation.

Chapter 4. Non-Social Activities

OUTLINE

A. INTRODUCTION

The behavior of fiddler crabs may be roughly divided into maintenance activities, defenses against predators, and social patterns. As usual in such classifications, and particularly in any subdivision of *Uca*, the dividing line is movable and a number of activities are multifunctional. Burrows provide an example. Seldom dug by the current occupant, they are nevertheless kept clear and, if necessary, enlarged by that individual. The burrows probably originated as an underwater defense against fish and other predators and continued as protection also against desiccation, heat, and terrestrial enemies during low tide, as the ancestors of fiddler crabs assumed an increasingly active intertidal life. Today, at least, burrows also play fundamental roles in social behavior.

The present chapter will be confined to brief descriptions of certain non-social activities, selected principally as a foundation for the consideration of social behavior. Categories will be listed in rough order, from the most generalized activities, such as walking, to those most characteristic of the genus. Comments on the more physiological forms of behavior, such as respiration, will be confined to aspects particularly associated with other *Uca* activities, or with its ecology. Throughout, for amplification of such basic patterns see Waterman, ed. (1960, 1961), Marler & Hamilton (1966), and contributions to the *Symposium on Terrestrial Adaptations in Crustacea* (Bliss & Mantel, eds., 1968).

The various ecological factors and endogenous rhythms concerned in the activities of fiddler crabs are discussed in the chapter on ecology (pp. 440ff.) and in the section on rhythms in social behavior (p. 504).

B. RESPIRATION

As in all ocypodid crabs, when *Uca* are wholly or partially underwater, water is drawn into the gill chambers on each side through the afferent orifice between the second and third pairs of ambulatories. From here it circulates around the gills and passes out through the efferent channel at the antero-external angle of the merus of the third maxilliped. During low tide the crab descends its burrow the bottom of which is either damp or under water, at irregular intervals.

A supplementary system of maintaining moisture in the branchial chambers during low tide is provided by the crab's habit of suddenly lowering the body against the ground. In this position the brushes of setae fringing the afferent orifice are brought into contact with the damp substrate and requisite moisture drawn up into the pericardial sacs.

In addition to its primary functions of bringing oxygen to the gills and preventing desiccation, the water circulating in the branchial chambers is concerned in two other activities. One of these is feeding, since the water is led through the rhythmic action of the mouthparts into the buccal cavity, where it helps separate coarse, inedible material from finer organic matter. This process has been described on p. 456.

Finally, respiratory water apparently is sometimes of use in making acoustic signals (p. 484).

Uca and *Ocypode* are the two most perfectly amphibious crustaceans. Of the two, *Uca* is the less terrestrial. Although tested species can survive indefinitely when completely submerged, the same forms die even in humid air after a few hours. Nevertheless, strongly displaying species and those that aestivate and hibernate must often be taxed, and doubtless then the crab relies on the air spaces in the epibranchial regions which are lined with blood vessels, as well as on moisture stored in the pericardial sacs.

The epibranchial regions probably also serve as resonating devices when appendages rub against the carapace during sound production (p. 483).

In the respiration category may be mentioned the aeration of eggs by ovigerous females. These individuals may be seen now and then, either crouching low or standing high, while masses of bubbles emerge from the branchial orifices at the third maxillipeds and pass backwards over the egg mass. Similar behavior, here termed *bubbling*, has been noted in both sexes kept in small containers when the shallow water becomes foul, and also in large terraria, where Schöne (1968) found it occurred regularly, apparently as a cleaning mechanism. Altevogt (1969.2) has presented evidence that bubbling is a temperature regulating mechanism. Finally, in the burrow bubbling sometimes functions as an acoustic signal (Crane, 1966 and p. 484).

C. LOCOMOTION

Since it is a typical crab, *Uca* walks sideways. Either the large claw or the minor may lead, depending on the social situation. Also, depending on the crab's phase, the body may be held very high, or slung low. A fiddler can run rapidly, in spite of its moderately short legs, but only for a few seconds at most. In many species the crabs are adept at changing direction and proceeding in brief dashes. Such speed and maneuvering are used only during emergencies associated with escape, combat, and courtship. Manton's pioneer studies on crustacean locomotion (especially those of 1952 and 1959) would make an excellent basis for a comparative study among the species of *Uca*.

D. FEEDING

To any human being who watches a fiddler crab eat, the feeding process looks simple. At low tide the crab sits on the shore with the buccal area almost vertical, the most posterior part being also the lowest. In this position the fiddler repeatedly scrapes up a bit of substrate in a small cheliped and places it between the inner edges of the third and second maxillipeds, held ajar during feeding. Males use the single minor cheliped, apparently at a faster rate than the two similar chelipeds of females, which use them alternately. Sometimes single scrapes are made, sometimes four or more at a time, before the material is carried to the mouth. There do not seem to be specific differences in this behavior; the number of scrapes is probably related to the character of the terrain. In general small crabs feed faster than large ones and, expectably, heat speeds the tempo. Displacement feeding motions and those combined with low intensity waving are predictably slower than the highly motivated gathering of substrate following a crab's emergence after high tide. Miller (1961) in his detailed examination of the feeding process, gives rates of routine feeding in several species. The course of the pinch of substrate within the buccal area, based principally on Miller's work, has been reviewed in this contribution starting on p. 456.

The spoor of active *Uca* in the Indo-Pacific may briefly be confused with that of other genera but can always be identified by the lines of pellets radiating from a burrow. The crab's habit is to move slightly ahead as it feeds, whether it is at the time a burrow resident or a wanderer.

The only detailed analyses of the pellets discarded in feeding and of fecal pellets have been published by Verwey, Altevogt, and Miller (all *loc. cit.*, p. 456). Verwey's work was in Java; Altevogt's analyses were wholly on *vocans*, near Bombay; Miller worked on species in the eastern United States. There is general agreement that microscopic algae and protozoans living in the substrate, as well as organic matter brought in by the tide, form the main items of diet. Diatoms, although often ingested, seem usually to be excreted.

The zoeae and megalopa are efficient predators of planktonic animals (Herrnkind, 1968.2, and refs.).

In addition, I often observed both *panamensis* (in Costa Rica and Panama) and *tangeri* (in Angola) supplement filter-feeding with the plucking of algae growing on stones. Furthermore, in the females of a number of species, such as *vocator* and *maracoani*, the pile sometimes appears to give support to living algae. In both these species and many others a plucking motion with the minor cheliped from the female's carapace plays a definite role in courtship (p. 503).

In Costa Rica I once saw *brevifrons* eating mammalian feces, although *Uca* certainly is not normally a scavenger.

When a male loses the minor cheliped, he attempts to use the major in feeding. If the degree of hypertrophy is not too great, he may successfully support himself for weeks or months, until regeneration is accomplished, as has been observed in the crabberies. Crabs losing both chelipeds bring the buccal region in contact with the substrate. No data are at hand to show the long-term success of this procedure.

E. DEFECATION

The anus is at the end of the abdomen; the small fecal pellets are deposited by a partial lowering of the abdomen. These pellets are smaller than the cylinders of substrate discarded at the posterior end of the third maxilliped and, once recognized, the two kinds of discarded matter cannot be confused. Large gobbets found near fiddler burrows are merely loads brought up during digging operations.

F. CLEANING ACTIVITIES

The major cleaning pattern is simply submersion. A crab muddied from digging will often emerge dripping and free of mud, after a brief descent into his burrow in which water is still standing, just before starting a display period. Cleanliness is definitely associated with the display phase (p. 687); crabs in other phases, particularly when in the wandering or early aggressive periods, sometimes do not remove mud except from the eyes and eyestalks.

Special cleaning motions, moderately well stereotyped, play roles both in actually removing mud clinging to parts of the carapace and appendages and in social behavior (p. 461). The eyes and their stalks are cleaned primarily by depressing them alternately into freshly wet sockets. Secondary agents are the distal, setose segments of the third maxillipeds and the serrations and setae of the minor chelipeds. The direction of the wiping motion, in contrast to that used in cleaning other appendages, is from the distal to the proximal end, doubtless as a means of avoiding the addition of mud from the stalk to the functional part of the appendage. Since this direction is contrary to the usual pattern in arthropod cleaning motions with which I am familiar, the very practical adaptation is of special interest. Mantids, for example, in cleaning their forelegs with their mouthparts, work from the proximal to distal ends of the segments.

The minor cheliped cleans the major, always spending most time and moving most often over the outer surface of the manus and chela. Sometimes it reaches within the gape to clean part or all of the outer pollex as well as, less often, the tubercles of the gape. Motions along the inner side of manus and chela are less frequent, and those against the carpus and merus unusual. The outer sides of the major merus and carpus, especially proximally, as well as of the minor cheliped and ambulatories, are cleaned principally by rubbing adjacent meri against one another. Among the ambulatories the other segments are used similarly, particularly the ambulatory dactyl.

In cleaning no specific differences are apparent. No usual sequence has been observed. All are well developed in the early crab stages. All are prevalent forms of displacement behavior (p. 520).

G. BASIC DEFENSE

This section concerns only defense against predators, which, in *Uca*, are restricted chiefly to birds, crab-eating raccoons, dogs, and human beings. Protection against ecological hazards are discussed starting on p. 451, and in the following section on burrow-digging (p. 474). Intraspecific agonistic behavior is treated in later chapters.

Against predators, actual or potential, the primary defense is a simple escape down a burrow, preferably the hole which the crab has inhabited for a longer or shorter period but, failing that, any one that can be reached by a brief run.

If a fiddler escapes into a burrow that is already occupied, the intruder will be tolerated by the resident, when acoustic signals fail to drive it out, until the intruder senses that it can emerge and go elsewhere. This behavior is further described under territoriality, p. 511. Repeated quick forays are made to the brink of the burrow, so that the eyes can briefly overlook the surface. Although none of the necessary experimental work has been done, part of the emergence signal is undoubtedly visual, the positive stimulus apparently being a lack of unaccustomed objects in motion. If the strange object, such as an observing human, remains motionless long enough, at a highly variable distance of toleration, the crab emerges in spite of the addition to the surroundings. It may also stay below in response to vibration signals, such as steps near the burrow. Populations of the same species and subspecies vary widely in their toleration distances. Groups that are frequently disturbed, such as populations beside roads or on village shores, are often expectably more tolerant. Populations in more isolated places are unpredictable; the reasons for the local variations could form a most rewarding study.

When a fiddler crab is pursued while feeding or wandering near the low-tide level at a distance from all burrows, it has available several lines of defense. First it may try to sink into the mud with a rotating motion. If the substrate is too firm for the crab to corkscrew downward but soft enough for easy excavation, the fiddler can quite quickly dig a burrow with the ambulatories. Obviously, there is rarely time for this activity in the presence of a true predator. I have, however, watched it occasionally when I have been the cause of the alarm. Again, such crabs sometimes escape threats by running into the water far enough to be wholly submerged. The final defense is the universal crab gesture of rearing back by folding the posterior ambulatories, simultaneously straightening the front legs to raise the front of the carapace, and spreading both chelipeds out, with the chelae open. If the crab is chivied when in this position with beak, paws, stick, or finger, the major chela moves to seize the threatening object.

A crab in its burrow sometimes seizes a similar thrusting threat in the same way; usually, however, it burrows downward as fast as possible, and grabs the intruder only when further digging is blocked.

Although some components of acoustic behavior may prove to be elicited only by potential predators, no example is yet known. On the other hand, sound production is a usual response of a burrow resident to small intruders, in particular to conspecific *Uca* (p. 485).

H. BURROWING

Although burrowing motions appear identical throughout the genus, it used to seem that good specific differences would emerge in the forms of the burrows. These characters doubtless do exist, but they have proved to be so dependent on ecological and seasonal conditions, and so much comparative work would have to be done in order to draw valid conclusions, that this kind of species-specific behavior will not be described here in more than general terms.

Takahasi, for example (1935), described what appeared to be typical burrows of *arcuata* and *vocans borealis* in northwest Taiwan. Investigations of the same locality showed in the spring of 1963 (Crane, unpublished) that, although the habitat investigated by Takahasi was optimal for *vocans*, it was not favorable for *arcuata*. Since the latter species lives typically in crowded populations in upriver mud, the burrows there are quite different from those of the sparse, atypical population living among *vocans* in muddy sand on the somewhat stony shore. Takahasi's method of taking plaster casts of numerous individual burrows seems to be the only one that would be altogether valid for detailed studies. Casts would, of course, have to be made of many groups of examples, from various levels on the shore and in various ecological and geographical parts of the range of each species.

In view of these requirements, it will only be said that most *Uca* appear to have simple burrows, proceeding diagonally downward. The deepest burrows, which may end more than three feet underground, are made by the larger individuals, in river banks and on shores near high-tide level, as well as by some aestivating or hibernating crabs. The shallowest, sometimes only two or three incres deep, are produced by very small species or by individuals in moist habitats. Enlarged niches are sometimes found in the shafts, as are, I think rarely, forks and more than one entrance.

Regardless of the direction or depth of the digging, the method is always the same. The crab digs only with the legs of the minor side, which precede the crab into the hole and curve around the excavated mass, forming a basket with the setae. All material from burrows is carried at least a short distance from the mouth and either dropped on the spot, or more rarely tossed away. The dropped loads are always much larger than the feeding pellet, but are often well compressed into balls.

A single exception occurs to the rule that males dig only with the legs of the minor side. In attempting to force another individual from a burrow, the intruder sometimes briefly thrusts his major chela below ground, making with it prying or scooping motions that rarely bring out a small amount of substrate or even successfully flip out a smaller crab. Usually the motions are ineffectual; it seems probable that the descending cheliped continues to act as a threat symbol, doubtless sometimes engaging the claw of the other male (p. 515).

Very young crabs do not make their own burrows, but when pursued escape into those of larger individuals, or simply sink into soaking wet terrain at the water's edge. Their first burrows are very shallow, and close to the low-tide level. The larger displaying males are typically found nearest to high-tide marks. The subject will be further discussed in the following chapters.

The burrow is often, but by no means always, stopped up with a plug of material from either the outside or inside before it is covered by the tide or in the midday heat. It has been suggested that a column of air is kept by this means in the burrow. This does not seem possible, since apparently nothing is done to line the burrow with waterproof material, save for a few notable exceptions; *lactea*, for example, in its sandier habitats, lines the shaft with wet mud from below. The releaser for the plugging behavior is wholly unknown.

I. ORIENTATION

The critical study of orientation in *Uca* has begun very recently. Altevogt (1963.1) showed how *tangeri* find their way back to a particular area of the beach, but not necessarily to their former burrows, by polarized light. A more general paper on orientation in *tangeri* followed (Altevogt & von Hagen, 1963). Herrnkind (1966, 1967, 1968.1, 1968.3) described similar behavior in *pugilator*. In both species the crabs use, as appropriate, polarized sky light, sun navigation, and landmarks for orientation at a distance. At close range, however, *tangeri* appear to find their burrows with the help of kinesthesia rather than vision (Altevogt & von Hagen, 1963).

J. LEARNING

Altevogt (1963.2) performed the first modern experiments on learning in *Uca* during his investigation of visual discrimination ability in *tangeri*. Using artificial burrows as rewards, he succeeded in training between four and six individuals in a total of 23 to select a particular direction, and to discriminate between lights of different intensities. He was unable to train any of the group to distinguish between colored lights of equal intensity or between lights of different planes of polarization.

Langdon (1971), after finding that shape discrimination is well developed in *pugilator*, concluded: "Training studies suggest that the preference for vertical vegetation-like stimuli is a learned one and is subject to modification to adapt to changing characteristics of the environment. However, these experiments do not rule out the possibility that innate components exist and cause a predisposition to prefer vertical visual stimuli. . . ."

K. SUMMARY

The non-social behavior included in this chapter consists of maintenance activities and defenses against predators. Most of the selected patterns clearly form the foundations on which are based patterns of social behavior. For example, territoriality depends on the habit of digging shelters in the intertidal substrate. The overt facets of respiration are reviewed, as are procedures in walking, feeding, defecation, cleaning, avoiding predators, and digging. Recent studies of orientation and learning are noted.

Chapter 5. Components of Social Behavior

OUTLINE

A. INTRODUCTION

In fiddler crabs, social behavior consists almost altogether of agonistic activities, their ritualized derivatives, and courtship. Most but not all aggressive behavior, whether ritualized or not, is also clearly connected with reproduction. With two exceptions—droves and synchronous waving—none of the patterns shows collaboration between more than two crabs in a joint activity. Fiddler crabs neither dig communal burrows, for example, nor threaten predators in unison. There is no trace of the group territoriality found especially in some mammals, where an area is defended by its inhabitants from trespass by another group of conspecifics. Furthermore, since the larvae are released at hatching, there are no mutual, behavioral responses between parent and mobile offspring, even to the extent found briefly in scorpions.

Yet, as described in the chapter on structures and functions, the specializations for threat, combat, and courtship are unsurpassed. Although fiddler crabs cannot be termed socially cooperative in any usual sense, they must, it seems, be vitally dependent on one another. The forms of this dependence remain unclear. As will be shown, males do not have to fight to obtain empty burrows. There is no visible struggle for food. There seems to be ample space in every population for courtship. Successfully breeding males do not seem to be congregated in the middle of leks, although quantitative work in this field has not been done. Combats with other males are not prerequisites enabling them to mate. Females are not attentive to encounters between males, nor do they select the brightest or most actively waving individual. In several subgenera, waving is not even always a part of successful courtship, although it always occurs during the breeding season in every population. Successful mating, even in subgenera in which courtship is elaborate, will take place in a finger bowl, with no preliminaries, no food, and no tide. Consequently, we seem to be left with the vague conclusion that both intermale behavior and waving courtship display serve under natural conditions as mechanisms for stimulating and synchronizing reproductive behavior in the population as a whole. They doubtless also discourage copulation by males not in optimal breeding condition. The single certainty is that we know almost nothing of the physiological mechanisms underlying these values.

As usual in social animals, some of the components in agonistic behavior and courtship are ambivalent. The most striking example is "waving," the motion of the large cheliped in males which, in most species, is an indispensable part of courtship and, in all species, is performed most rapidly and vigorously during courtship. Waving is also an important part of threat behavior which, in fact, almost certainly underlies much of the evolution of the wave. Recent investigations are bringing to light increasing numbers of examples where the same means of sound production is used in both aggression and courtship. The structures sometimes built outside fiddler burrows are probably similarly ambivalent.

In the following pages, the general repertory of social components will first be enumerated. The great majority are concerned with agonistic behavior, not with courtship. They will be divided, for convenience rather than from evolutionary logic, into seven groups: first, droves; second, agonistic postures and associated motions; third, sound components, both known and probable, in threat and courtship; fourth, combat components; fifth, the components of waving display; sixth, constructions beside burrows; seventh, copulation. Subsequently, rhythms and phases of social activities will be considered, along with examples of unusual behavior.

For general accounts, with bibliographies, of the bases of social behavior in animals, see Marler and Hamilton, 1966, Eibl-Eibesfeldt, 1970, and Hinde, 1970; for reviews of social behavior in Crustacea, see Schöne, 1961 and 1968.

B. DROVES

In the lowest rank of fiddler sociality belong the kinds of behavior grouped here under *droves*, a term occasionally applied to moving aggregations of *pugilator* in the southern United States. No driving or herding of the crabs is implied. Like numerous other moving groups in the animal kingdom, including schools of fish and traveling caterpillars, the individuals in fiddler droves take no apparent notice of any particular individuals. Although their formation changes rather freely, they do move as a crowd, in a roughly similar but easily altered direction, and may stay together throughout almost an entire period of low tide. All of this behavior is in contrast to the types of social behavior which will be described later.

The droves of *pugilator* have been familiar to naturalists, children, and, unfortunately for conservation, commercial collectors for a long time. Thanks to Herrnkind's recent work (1968.3 and refs.) on visual orientation in the species, this part of *Uca* behavior is at last receiving modern professional attention.

Droving appears to be of at least two distinct kinds, representatives of both of which were noticed by Herrnkind in the course of his study. In the first, feeding aggregations of both sexes move down from the upper beach to low-tide levels. Second, "small groups of either sex occasionally migrate along the shore for considerable distances, up to 100 m, and apparently establish residence in new localities."

The first class occurs, as Herrnkind points out, in populations of the species holding burrows high up on the beach, rather than among those living and feeding on flatter shores. As in all other species of *Uca* with which I am familiar, individuals with burrows on the higher levels, where the food supply is less rich, often come down to feed at the water's edge. Droving becomes conspicuous in many *pugilator* populations because they are adapted to relatively sandy habitats, the upper levels of which are poor in microorganisms compared with lower levels, so that great numbers of crabs, "from a few dozen to thousands of individuals" (Hyman, 1922) sometimes move down to feed.

The second class is of greater interest from a social point of view. These crabs, consisting only of males in the examples I have observed, move more as an associated group. They may or may not spend much of their time feeding. In *pugilator*, the only droves I saw during brief observations near Miami, all consisted of males behaving as do single tropical males in the non-aggressive wandering phase, except that they moved almost as a unit. The members almost touched one another, feeding below the levels of the burrows as in the mixed groups of the first class but along a strip starting a few feet farther along the beach than the nearest holes. No droves formed of both sexes, or of females, occurred in this population. When they were startled by me the males stayed together, moving obliquely away toward the water, then surging back a few moments later.

I have watched large droves composed wholly of males in four other ocypodids, in *Uca tangeri* in Angola, *Dotilla* spp. in Zanzibar and western Australia, and *Myctiris* (soldier crabs) in Brisbane. In each, the individuals numbered between 500 and 1,500. In *tangeri* and in both observations on *Dotilla* the droves appeared only in conjunction with spring tides, which of course uncovered more potential feeding area than was usually available to them. Two points in this connection are interesting. First, these tides occurred in the morning, in correlation with a natural peak of *Uca* social activity (p. 505). Second, except in the case of Zanzibar *Dotilla*, the crabs did not proceed beyond the usual limits uncovered, although they did not avail themselves of this area on other days. Fortunately Cameron (1966) has provided a season-long study of drove behavior in Australian *Myctiris*, such as is greatly needed in *Uca*. In fiddlers the corresponding pattern is so little known that no further reference to it will be made in later sections.

It is worth noting here that I did not see any shore bird, the most usual predator on fiddlers, pay apparent attention to the large and conspicuous droves of the second class described above, much less seize a crab.

C. AGONISTIC POSTURES AND ASSOCIATED MOTIONS

Certain postures are prevalent in *Uca* during territorial, aggressive, and submissive behavior. Most of them will probably prove to be characteristic of the entire genus; others appear to be confined to several subgenera. These postures all may and usually do continue as equally typical motions. They do not follow one another in fixed sequence, although their occurrences and order are sometimes predictable in a given social situation.

The postures and their associated motions, described below, will be given names suggestive of their form.

1. *Raised-carpus.* Male. A low intensity posture. The mano-carpal joint of the flexed, major cheliped is raised, with the fingers ajar and pointing obliquely down. Sometimes the carapace on the major side is also slightly raised. The raised joint is usually pointed toward a nearby male that is either approaching from a distance or encroaching on the feeding area of the posturing individual. More rarely, it is aimed towards a crowding female or a member of another species, especially when all are feeding in a closely spaced population. The posture is sometimes accompanied by the vibration of the major merus against an adjacent part of the carapace (p. 482). (Fig. 84 *A*, *B*, *E*.)

2. *Down-point.* Male. High intensity threat often leading to combat. Apparently a direct derivative of the raised-carpus, which, however, does not necessarily precede it. It has been observed in only four species, *tangeri* (subgenus *Afruca*), *maracoani* and *ornata* (both in the subgenus *Uca*), and *pugilator* (*Celuca*). The posture is characterized by the extreme vertical position of the chela. The finger tips usually touch the ground immediately in front of the crab while the mano-carpal joint is maximally raised. Frequently, two potential opponents approach each other closely before both, almost simultaneously, assume the position. High intensity combat with linked chelipeds sometimes follows immediately.

3. *Frontal-arc.* Male. Low intensity. Similar to the raised-carpus, except that the flexed cheliped, fingers slightly to widely apart, is entirely parallel to the ground and almost touches it. Although the posture is sometimes held for moments at a time, the claw usually sweeps slowly forward and back in a small arc. It occurs frequently in a crowded feeding situation and the actor often does not interrupt the rhythm of his minor cheliped.

4. *Forward-point.* Male. Moderate intensity. Uncommon. The major cheliped, held low and level with the ground, is half unflexed, so that the wide-open chela points forward, toward an approaching opponent.

5. *Lunge.* Male. High intensity. Often follows a raised-carpus or forward-point. With the major cheliped partly flexed, the crab makes a feint toward a potential opponent, the body and cheliped being thrust suddenly in the direction of the other crab while the ambulatories shift position little or not at all.

6. *After-lunge.* This motion appears identical with the lunge and is separated from it here only because of its close association with combat, and because the name was used in an earlier contribution (Crane, 1967). The after-lunge often follows an encounter so closely that it may prove desirable in the future to term it a full component of combat.

7. *Carpus-out.* Male. Usually follows a raised-carpus. The crab, at the continued approach of a potential opponent, sometimes partly withdraws into his burrow, leaving the still-flexed cheliped protruding more or less above the ground, the mano-carpal joint still highest.

8. *Flat-claw.* Male. A partially withdrawing crab frequently leaves the entire manus and chela perfectly flat on the surface. (Fig. 84 *H*.)

9. *Chela-out.* Male. A third posture occasionally assumed in partial withdrawal occurs when only the extreme tips of the fingers remain above ground, ajar and pointing straight up.

10. *Lateral-stretch.* Male. This position is typical of burrow-holders, is almost certainly ubiquitous in the genus, and occurs with great frequency. In earlier contributions (Crane 1957, 1966) it was called the "lateral threat posture." The major cheliped is widely outstretched, either far to the side or obliquely forward. The minor cheliped may or may not be similarly extended. The stance is reserved in social behavior for threat toward a potential opponent passing either to the rear or obliquely to the side; it is sometimes accompanied by vibration or rubbing of the major merus against the side of the carapace (p. 482). This posture corresponds to the classic threat position found in many kinds of crabs and perhaps occurs in all brachyurans; Schöne (1968) gives examples of this and similar postures in a variety of forms. In the field I have observed it in the portunids *Portunus* and *Callinectes*, in many xanthids such as *Carpilius*, *Xanthodius*, and *Menippe*; in the grapsid genera *Grapsus*, *Pachygrapsus*, and *Sesarma*; in the potamonid *Pseudothelphusa*; in the gecarcinids *Gecarcinus* and *Cardisoma*; and, finally, in various ocypodids other than *Uca*. All of these crabs, as well as *Uca*, when cornered or overtaken by predators or humans, may give this response. (Fig. 84 *F*.)

11. *Creep.* Male. A crab in neither an aggressive nor a display phase often walks past displaying males with the body held rather low; occasionally, but not always, the minor side leads. The same behavior is sometimes accentuated when the crab has been physically overturned in a forceful fight, or has had his burrow taken from him. At these times the sternum barely clears the ground. (Fig. 84 *C*.)

12. *Prance.* Male. Several species have been observed walking stiffly with their dactyls turned under. Some-

times the behavior occurs in an obvious intermale threat situation; sometimes no potential opponent is in sight. It seems likely that the odd method of walking may produce sounds through stamping; the stimulating crab may well be underground.

13. *High-rise.* Male and female. Both sexes sometimes raise their bodies high on their extended ambulatories, some of which often do not touch the ground. The posture in males is often associated with waving, in both threat and courtship. In females the stance indicates unreceptiveness and is usually accompanied by ambulatory stridulation (p. 482). Her stiffened legs and increased height make it difficult or impossible for the male to grasp and turn her into the copulatory position.

14. *Legs-out.* Female. A frequent form of unreceptive behavior. The female partly descends her burrow, leaving the legs of one side projecting stiffly upright in the air or obliquely out. This action effectively blocks the attempts of the male to dislodge her or, when her burrow is large enough, to follow her below. (Fig. 89 *A*.)

D. SOUND PRODUCTION

1. *Introduction and Historical Review*

Reviews of mechanisms for sound production in crabs have been contributed by Guinot-Dumortier & Dumortier (1960) and by Dumortier (1963). They present a wide variety of mechanisms, almost all stridulatory in nature, in nine families of brachyurans. Sound has been actually detected in few of these species, but the specializations are so apparent that there seems to be little question but that sounds can be elicited and recorded as soon as investigators give attention to the problem. Most of the mechanisms consist of a series of close-set parallel ridges or slightly raised striae which are readily rubbed by or against a row or cluster of tubercles; the latter structure is often less specialized than the parallel ridges. Most of the examples given concern the following pairs of opposable parts of brachyuran anatomy: (1) suborbital region against merus or carpus of cheliped; (2) pterygostomian region against manus or dactyl of cheliped; (3) third maxilliped against cheliped's dactyl; (4) one segment of the cheliped against another; (5) cheliped manus against part of an ambulatory; (6) part of one ambulatory against part of another.

The production of sounds by ocypodids was first reported by Alcock (1892) and Anderson (1894) after they heard stridulation in India from burrows of two species of *Ocypode*. Suspected in *Dotilla* by Aurivillius (1893), sound production was confirmed more than sixty years later by Altevogt (1957.2). It was suspected in *Ilyoplax* and *Macrophthalmus* by Tweedie (1954). Stridulatory motions have been observed and photographed, but not tape-recorded, in both these genera by Crane (unpublished). Finally, *Ocypode gaudichaudii* has been heard producing sounds when in its burrow (Crane, 1941.2).

Dembowski (1925) first reported sounds from *Uca* when he worked on *pugilator* in the eastern United States. Rathbun (1914.2, 1918.1) described juxtaposable ridges and granules, which she presumed must be stridulatory, on the major manus and first ambulatory in *musica.*

Crane (1941.1, 1943.3, 1957) mentioned the possibilities of sound production in courtship, threat display, or both in the genus. The mechanisms suggested were stridulation and "rapping" on the ground with the major cheliped. Three other species, *inaequalis*, *beebei* and *terpsichores*, were shown in the 1941 contribution to have specializations similar to those of *musica.* In the same three references, rappings on the surface of the ground beside the burrow were reported as visible elements in certain species-specific courtship displays. These species were *inaequalis*, *cumulanta*, *batuenta*, *saltitanta*, and *pugilator*.

Meanwhile, Burkenroad (1947) reported on the use of sounds by *pugilator* in nocturnal courtship. He found that during darkness drumming or knocking underground replaced waving as a stimulus to the female. Burkenroad did not then believe that the ground was actually hit at the mouth of the burrow by the cheliped during visual display during the daylight.

In 1959 Altevogt reported work on sounds made by *tangeri*, as part of a detailed study of the ethology and ecology of that species in southern Spain. The sounds were considered to be primarily part of nocturnal courtship, and showed a correspondence in rhythm with that of diurnal waving. They were of two kinds, a long whorl and a short. When drumming was made on the surface of the ground by a crab above the burrow of another crab, it served as "an irresistible signal for the occupant to come out."

So far none of the observers had yet obtained tape recordings of sound production by any species, whether actually already heard by human ears, or suspected through morphological and behavioral clues.

Recently the subject has been actively pursued with rewarding results. Salmon and Stout (1962) published an analysis of tape recordings of *pugilator* in their burrows, and once more reported vibration against the burrow's rim. In the same year Altevogt and von Hagen published analyses of records of the populations of *tangeri* they were continuing to study in Spain.

Since those first studies, additions to the list of species shown by tape-recordings definitely to produce sounds have increased yearly, through the work of

Salmon (1965, 1967) and Salmon & Atsaides (1968.1, 1968.2) in the United States, Crane (preliminary report, 1966) in Trinidad and the Indo-Pacific, and von Hagen in Trinidad (preliminary report, 1967.2). At present, the number of species so recorded is about 20, with every subgenus represented except *Amphiuca.* Morphological and observational data give less complete evidence for other forms. There remains, in short, no question whatever but that sound plays an important role in social behavior throughout the genus.

The preceding sentence is now the only general statement on sound production in *Uca* that can be made without hedging. The numerous means by which sounds are produced, the range of variation of their acoustical characteristics, the stimuli that elicit them, and their functions are just beginning to be understood. The sensory receptors are still unknown. There is even disagreement on the medium carrying the stimuli, since all stimuli may be perceived through substrate vibrations, as seems likely to von Hagen (1962), or some may be airborne, as considered highly probable by Salmon (1965, 1967). Investigation of the subject continues (Horch & Salmon, 1969).

Rapping or drumming, as reported in contributions through 1962, was apparently done by vibrating the flexed cheliped against the ground; this took place at the burrow entrance and, it was suggested, when the crab was underground. In a preliminary report in 1966, Crane listed tape-recordings of sounds made not only by the usual drumming but also by rubbing the ambulatory meri together, by vibration of membranes at the base of the minor cheliped, and by emission of bubbles from the efferent branchial channels; examples of these were played back at the 1965 Ritualization Discussion; Pl. 47 of the current contribution is the first published record of the oscillographs. Meanwhile, Salmon (1967) reported ambulatory vibration as distinct from stridulation by Florida species of *Minuca*, and published representative oscillographs; he was then of the opinion that this behavior was subgenerically typical, while drumming of the cheliped seemed restricted to *Celuca* (*pugilator*, *speciosa*). Von Hagen's 1967 contribution, a preliminary report, lists the species he recorded in Trinidad, but does not comment on the methods of sound production or include oscillographs. Finally, Crane (1966, 1967) reported that the sounds of ritualized combats between males are sometimes audible to man; not one of them has yet been recorded.

All the investigators agree that *Uca* sounds so far recorded are of low frequency and that the tempo increases with a rise in temperature. The contributions of Altevogt and von Hagen, and of Salmon and his co-workers, agree that sound production replaces waving as a part of courtship, both under certain conditions when the crab is underground and at night. In addition, von Hagen (1962), enlarging on Altevogt's original observation, described for the first time an aggressive element in the drumming of *tangeri.* When a burrow-holder emerged at night in response to drumming on the surface by a passing male, two results might follow. If the emerging crab was a female, copulation might ensue, but if another male, aggressive behavior could follow. All investigators agree that spontaneous sounds at night are usual in several species now acoustically familiar. Altevogt (1964, 1970) showed that in (*Afruca*) *tangeri* and (*Celuca*) *inaequalis* antiphonal drumming may be elicited. This behavior resulted when he tapped a finger on the surface of the ground close to the mouths of burrows occupied by male. Crane (1966) remarked that sounds can be most easily elicited by an observer by arranging for a conspecific male to enter a burrow occupied by another male. Salmon (1967) and Salmon & Atsaides (1968.1) also report successful use of this technique.

Recently, my reexamination of morphological specializations and of motion picture films, as well as further field observations, and video-tape-recordings have all led me to believe that sound production in general functions primarily in intermale behavior and in behavior by unreceptive females, while its use in courtship, at least on the surface, is more restricted. This viewpoint will be amplified in later sections.

II. *Components of Sound Production in* Uca

The means of sound production, known and suspected, in fiddler crabs divide conveniently into a number of categories and subdivisions, containing, in all, a minimum of 16 components. Several of these components are clearly compound, but in the present state of our knowledge it is impractical to fracture them further. In the present section, each component is provided with a short name, for ease of use in later sections, and briefly characterized. Descriptions of morphological and operational characteristics are given in more detail throughout Chapter 3 on Structures and Their Functions. A relevant page number is given at the end of each component description. Table 12 gives a utilitarian—not a phylogenetic—classification of these components and records their known occurrence in the genus, along with the kind of evidence at hand for including them.

III. *Sound Production by a Single Individual*

(*a*) STRIDULATION

The term stridulation will be used in its narrow sense. This will confine it to sounds heard, tape-recorded, or suspected that result from the juxtaposition, with rubbing, of two anatomical parts of the same individual. Components in which one part is tapped or vibrated ("drummed") against another part are placed in the next category (*b*). Guinot-Dumortier & Dumortier (1960) applied to Brachyura in general a nomenclature essentially the same as that long used in Orthoptera, where each kind of apparatus is divided into a *pars stridens* and a *plectrum.* The *pars stridens* is typically a series of striae or other elevations moved against an opposable ridge or sharp edge forming the *plectrum.* In *Uca* the distinction is often unclear or even wholly inapplicable; hence these otherwise useful terms will not be used in this contribution.

1. *Major-merus-rub.* The antero-dorsal or postero-dorsal armature on the merus of the major cheliped rubs against some part of the adjacent armature of the carapace. The suborbital crenellations, antero-lateral angle, antero-lateral margin, and perhaps the pterygostomian and subbranchial regions are the most probable structures involved. The rubbing appears typically to be a back-and-forth motion, but the details have not been worked out; doubtless the direction of rubbing depends on the alignment of the particular underlying structure concerned. In a few instances, a distinctly circular direction to the rubbing motion shows clearly in film sequences. Whether rubbing by the antero-dorsal or postero-dorsal surface of the merus takes place seems usually to depend on the position of the crab toward which the threat is directed. For example, when a potential intruder is passing behind a burrow-holder, the latter often extends the major cheliped in a lateral-stretch (p. 479), and may simultaneously perform a major-merus-rub; here his postero-dorsal armature rubs against the nearest part of the carapace, which in this instance will probably be the antero-lateral margin. Sometimes this component is performed when the burrow-holder is part-way down a hole, with the flexed cheliped and adjacent anterior carapace projecting.

In a single film sequence, showing two *deichmanni* facing each other, the crabs each made a major-merus-rub, one after the other, repeating the alternation several times without pause. This is apparently the only example yet at hand of antiphonal behavior during rubbing components.

The strongest part of the antero-dorsal meral armature is always distal. This portion of the merus, however, can come into contact with the carapace only in young crabs, because of the later effect of allometric growth. Any other function of the region in mature crabs is not yet known.

The component is so far known only in threat situations. Observed frequently in the field; filmed. Pp. 452, 457.

2. *Minor-merus-rub.* Similar to the major-merus-rub in form and use. Details unknown. Filmed only. Pp. 454, 461.

3. *Minor-claw-rub.* The manus and chela, or the chela alone, of the minor cheliped rubs against the suborbital crenellations. Details unknown. Filmed in one species only (*deichmanni*), but observed fairly often in the field. P. 461.

4. *Palm-leg-rub.* Structures on the anterior side of the first ambulatory adjacent to the major cheliped rub against, or are rubbed by, structures on the lower proximal triangle of the major palm. Known only in the subgenus *Celuca,* almost entirely by inferences drawn from the morphological specializations. These are best developed in six species. A film made by David Blest of *inaequalis* forms the only record to date of the structures in use. Here, between stages of a combat between two males, the first leg of one crab reaches forward and rubs against the proximal lower palm of his own cheliped. Pp. 458, 462.

5. *Leg-wag.* Structures, principally on the meri of ambulatories, rub against one another (Fig. 85 *A*, *B*). Rarely, the first ambulatory merus also rubs against, or is rubbed by, the merus of the minor cheliped. Both sexes behave similarly, the action being extremely common throughout the genus and usually occurring close to the mouth of the stridulating crab's burrow. It forms the most widely used threat pattern of females, in which this armature is always notably stronger than in their conspecific males. Often it forms part of the rejection pattern of unreceptive females.

Salmon (1967) and Salmon & Atsaides (1968.1, 1968.2) have recorded sound produced by similar leg motions in males of several species of *Minuca* in Florida. It appeared to these investigators, however, that the vibrating legs did not come into contact with one another, the sound apparently being made by their passage through the air as they vibrated in the dorso-ventral plane. The frequencies recorded also proved lower than would be expected from stridulatory mechanisms. The vibration occurred between contacts of the legs with the ground, which produced sounds of higher frequency (see the leg-stamp component, p. 484). During diurnal courtship the vibratory motions apparently sometimes followed the curtsy component of waving display (p. 496), just after the male had attracted a female close to the burrow mouth, curtsied with leg-stamps, and descended. At these times sounds were made that were similar to those recorded from leg vibrations made on the surface at night; because of the crab's position underground, however, diurnal tape-recordings were indistinct. Nocturnal sound production occurred both spontaneously and by experimental elicitation through tactile stimuli of various kinds, as well as by scratching the surface of the ground near the burrow with a twig. The investigators also found that in *rapax* a male sometimes increased his rate of sound production when another male was artificially stimulated. Differences among the species occurred in the duration of sound, intersound intervals, and number of pulses per second.

In the films made in connection with my own observations, leg-wagging appears in more than 20 species, but always inadvertently, since its daytime occurrence is sporadic, sudden, and almost always of brief duration. It has been tape-recorded in daylight on the surface in (*Thalassuca*) *vocans* and (*Celuca*) *lactea* (Crane, 1966); both of these examples were males in threat situations. (Pl. 47). Finally, during 1969 in New Guinea (Crane, unpublished), video-tape-recordings were made of the leg-wagging of burrow-holding *lactea* when approached by aggressive wanderers; for the first time we have definite proof of the synchrony of leg-wagging motions with sound production, along with evidence of the social situation in which the behavior occurs.

In fact, according to all my observations of leg-wagging, its function in daylight, above ground, appears always to be a part of agonistic behavior; often it appears in conflict situations. Judging by the similarities of sound, it almost certainly occurs as one of the warning signals underground in the presence of an intruder. Stridulations of this kind apparently rarely if ever play a role in normal courtship during daylight. However, since similar movements of the legs are often a part of waving display, as used in both threat and courtship, it is sometimes difficult or impossible to decide, even from a well-exposed film, whether the surfaces of adjacent legs actually come into contact, or whether the motion is ritualized, as described on p. 524, into a purely visual signal. The nocturnal vibrations described by Salmon & Atsaides (*loc. cit.*) are very much faster than the slow movements of ritualized wagging. P. 463.

6. *Leg-side-rub.* The meri of the more posterior ambulatories apparently rub against the antero-lateral, dorso-lateral, or vertical lateral margins, or the postero-lateral striae, of the carapace. Filmed only, the juxtaposition showing with certainty in only one species. P. 463.

(*b*) VIBRATION AGAINST CARAPACE

7. *Major-merus-drum.* As in the major-merus-rub, noted under 1 above, except that the motion is a series of rapid blows instead of a rub. Details remain unclear, but the smooth proximo-anterior surface of the merus strikes rapidly and repeatedly against the carapace, apparently on the outer pterygostomian or subbranchial region. The sound may well be amplified by the overlying airspace. All of the species so far known to make this motion are among those equipped with the deep bodies and expanded branchial chambers adapted for prolonged exposure to air. Known only in threat situations. Easy to confuse, during field observation and casual inspection of film, with the major-manus-drum (component 9, below). Filmed and tape-recorded. Pp. 453, 457.

8. *Minor-merus-drum.* Similar to preceding component, but performed by merus of minor cheliped. So far observed only in males. Filmed. Pp. 460, 461.

(*c*) VIBRATION AGAINST SUBSTRATE

9. *Major-manus-drum.* The proximo-ventral part of the manus of the major cheliped strikes repeatedly against the substrate. This is the first recognized and most familiar of the sound-producing components. It has been called by several terms: *trommelwirbel* and *wirbel* by Altevogt and by von Hagen; *vibration* and *drumming* by Burkenroad; *rapping* by Crane and by Salmon, Salmon & Atsaides, and Salmon & Stout (all references *loc. cit.*). All the terms refer to striking the ground rapidly, usually several or more times in a series, with the lower proximal part of the major manus or sometimes with the entire lower edge of the propodus. The term *drumming* will be used in this contribution, as the most descriptive term in English.

In drumming, the major cheliped is usually strongly flexed. The only discernible morphological specialization is an occasional enlargement of the proximal, ventral part of the manus (Fig. 85 *C*). Such an enlargement is not present in all species now known to drum, and on the other hand it is strongly developed in some of those forms in which drumming has not yet been detected (Pl. 22 *C*).

Drumming is known to be used in both threat and courtship, both by day and by night, on the surface beside the burrows at night as well as partway inside. It has been variously described, filmed, and tape-recorded by the investigators concerned in the studies cited on pp. 480-485, as well as in the course of the present work. During the latter I have watched and photographed drumming on the surface in *urvillei*, *vocans*, and *lactea* in the Indo-Pacific, as well as in *tangeri* in Portugal and Angola, and *pugilator*, *speciosa*, and *cumulanta* in the western Atlantic. In addition, I now have tape-recordings which appear to be the result of underground drumming in *dussumieri*, *coarctata*, *tetragonon*, three subspecies of *vocans*, and two subspecies of *lactea* in the Indo-Pacific. M. Flinn and I, working together, have also secured recordings of underground drumming in *vocator* and *cumulanta* in Trinidad; in each species recorded, the crab was drumming so close to the mouth of the burrow on one or two occasions that the vibrating cheliped was fully visible during the recordings; in these cases, therefore, there is no question that another means of sound production might have been responsible for the result.

The major-manus-drum is easy to confuse, as remarked above, with the major-merus-drum (component 7). P. 458.

10. *Minor-chela-tap.* The tips of the pollex and dactyl of the minor cheliped strike rapidly, several times in succession, against the substrate. Seen on film only, apparently in threat situations. P. 461.

11. *Leg-stamp.* In threat situations, the dactyls of two or more ambulatories are turned under and the crab in walking raises them higher than usual and brings them forcefully down; known only in film, but in all probability sounds with a signal value are produced. Similarly, in the threat movements termed lunges, after-lunges, and prances (pp. 479-480), acoustic signaling may well be involved. Finally, in high intensity threat and courtship, when some species lower the body in the component termed the curtsy, the legs during some curtsies make a stamp similar to that described above. Salmon (1967) and Salmon & Atsaides (1968.1) secured tape-recordings of the resultant sound. They also found that some of the multiple pulses obtained from leg-wagging were preceded by single pulses marking the momentary touching of the ground by the legs otherwise raised during vibration. P. 463.

(*d*) SOUND CONNECTED WITH RESPIRATION

12. *Bubbling.* This method of sound production seems to be unquestionably under the control of the crab, and to serve as a warning signal to intruders. The sound is produced by bubbles of air, enclosed by water from the gill, that appear rhythmically from the efferent branchial orifices at the distal outer corners of the meri of the third maxillipeds. The bubbles are not nearly as profuse and extensive as those occasionally produced by ovigerous females, perhaps for cleaning and aerating the eggs, and by both sexes in a number of grapsoids, used sometimes as a cleansing agent (Schöne & Schöne, 1963) and sometimes as a regulator of body temperature (Altevogt, 1969.2).

At present bubbling in the current sense is known to occur only in *maracoani* (subgenus *Uca*). Judging by the similarities of sound produced in the burrow under similar conditions, it seems probable that it occurs also in *Minuca.* Work on this signal is in a very preliminary stage. It may prove to be the most generally distributed of all warning signals, since no specialization at all, except for the control of the bubble formation, seems to be needed. Tape-recorded in males. Not yet tested in females. P. 472. A similar mechanism has been reported by von Hagen (1968.1) in *Ocypode* and in two species of *Sesarma* (Grapsidae). The resultant hissing (*zischende*) serves as a threat signal.

13. *Membrane-vibration.* A very different signal is also made partly by means of the respiratory apparatus. Here water, or air and water, from inside the epibranchial chambers is vibrated against the membrane at the base of one or both chelipeds. Striations in the membranes, clearly visible only in life, appear to be species-specific, as are the sounds produced. These have been observed and recorded outside the burrow, when the crab was held under a dissecting microscope; identical sounds in response to intruders were recorded from within the burrows. So far, this vibration of the membranes has been observed with certainty and recorded only in males of *vocator* and *rapax,* both members of the subgenus *Minuca.* P. 165.

IV. *Sound Produced by Contact between Two Crabs*

14. *Claw-rub.* Always by the major chelipeds of two males during combat. The term given here is broken down into distinct components and described in the section on combat, starting on p. 488.

15. *Claw-tap.* The remarks concerning component 14 apply.

16. *Interdigitated-leg-wag.* Two males or two females sometimes line up beside each other, with at least the more distal of their ambulatory segments in contact, and, sometimes, vibrating. Threat situations only. Observed in field but neither filmed nor tape-recorded.

V. *Characteristics of Sounds Produced by* Uca

It seems clear from the preceding section that acoustic signaling devices in *Uca* are more varied than in any invertebrate group so far investigated. Because this study is still in its active infancy, remarks on the characteristics of the sounds will be only illustrative and accordingly brief.

The sounds so far recorded on tape in studies of the genus all consist of rhythmic pulses, or groups of pulses, of low frequency. Examples of resultant oscillograms appear in Pl. 47. Detailed analytical work on sounds produced by other members of the genus has been done by Altevogt and von Hagen, using populations of (*Afruca*) *tangeri* in Spain, and by Salmon and his associates on a number of species in the United States. These investigators, in references cited below, agree that almost all the characteristics of each of the sounds vary widely. The variations appear in response both to temperature and to the social or experimental situation prevailing at the time of the recording. The figures that follow were extracted from the detailed data given in their contributions; they are presented in order to show the general nature of the characteristics involved and of their ranges of variation.

Altevogt (1962) and von Hagen (1962), when they examined the two kinds of whirls (major-manus-drums) made by *tangeri*, found the following characteristics. The short whirl consisted of 1 to 4 beats (that is, contacts of the manus with the ground), while the long whirl ranged from 7 to 12 beats. Each short whirl lasted about 0.5 second, while the long whirl extended over a period of 0.84 to about 2 seconds. The intervals between short whirls ranged from 0.8 to 1.4 second with the intervals between single beats ranging only from 0.8 to 0.10 second—a notably constant character. The intervals between short whirls were found to be equal to those between single waves during daylight under comparable conditions. In long whirls, single beats ranged from 0.12 to 0.16 second; long whirls were not repeated at regular intervals.

Salmon & Stout (1962) and Salmon (1965) found that in the corresponding component in (*Celuca*) *pugilator* the rapping (major-manus-drums) consisted of only one type, not a long and a short whirl. The number of pulses (beats) in each sound (rapping; drumming) ranged from 2 to 11, intervals between sounds from about 0.3 to more than 5 seconds, and the rate of production from 3 to 32 sounds per minute.

Recently (1971), Salmon showed that these manus-drum sounds made by *pugilator* contained maximal energies between 600 and 2,400 Hz. In contrast, sounds of "honking" made by uncertain means (present contribution, below and p. 195), which he recorded from (*Minuca*) *rapax*, contained maxima between 300 and 600 Hz. He also reported that *rapax* proved significantly more sensitive to vibrations between 480 and 1,000 Hz than was *pugilator*. Additional related contributions are those of Salmon (1967), Salmon & Atsaides (1968.1, 1968.2, 1969), and Horch & Salmon (1969).

To human ears, the sounds produced by *Uca* fall very roughly into four categories: first, those of a rasping nature, probably resulting from conventional types of stridulation where one surface of a crab is rubbed against another; second, sounds resulting from the various types of vibration; third, the rhythmic, hollow noises that appear to originate from mechanisms based on the respiratory system; and, finally, distinct series, always from underground, of unknown origin. The most characteristic of these unknown noises, called *honking* in the description of *rapax* behavior (p. 195), is not included in the table; the mechanism may well prove to be one already listed.

To me, it seems highly probable that male *Uca* of at least most species can make at least three different signals, using wholly different mechanisms and excluding any acoustic signals resulting from combat. In some *Celuca*, the number is doubtless higher. The repertory of *deichmanni*, for example, includes five apparent acoustic signaling motions, all of which appear on film, although they have not been tape-recorded. These are the major-merus-rub, minor-claw-rub, leg-wag, major-manus-drum, and minor-chela-tap (components 1, 3, 5, 9, and 10). It seems likely that one or more components, perhaps including mechanisms not yet suspected, are usually restricted to sound production underground.

Although some of our tape-recordings of *cumulanta* in Trinidad resulted from the introduction of a conspecific male as stimulus, others reproduced a resident male's drumming at the burrow mouth during courtship. As in the cited work of Altevogt, von Hagen, Salmon, and co-workers concerning other species, these surface drummings were closely similar to subsurface sounds elicited by male intruders. In the case of *tangeri*, it will be recalled, identical drummings on the surface by a passing male could elicit either aggressive or courtship behavior depending on the sex of the emerging burrow-holder, according to von Hagen (1962). In a film of the same species I made in Angola, an aggressive wanderer induced a burrow-holding male to emerge and give up his burrow merely by drumming on the surface; no combat ensued; instead the dispossessed crab promptly departed in the creep position (p. 121).

These examples indicate that social sound production, as with other branches of *Uca* behavior, is undoubtedly ambivalent.

E. Components of Combat and Their Organization

I. *Introduction*

Preliminary Note. Much of this section is taken directly from an earlier paper on the subject (Crane, 1967). An exception, aside from minor alterations, is the description of additional components of combat, resulting from field work done between 1968 and 1970. Further laboratory work has also led to a better understanding of the relations between individual structures on the claw and their uses in combat. This aspect has already been reviewed in the section on the morphology of the major cheliped, beginning on p. 456. Tables 13 and 14 show the distributions of structures and components as they are known today. The locations of the structures are shown in Figs. 42-44. A contribution on results of the recent field work is in preparation and will be published separately.

Male fiddler crabs sometimes seize each other's large claws at the climax of a fight. Physical damage practically never occurs, although the stronger sometimes flings the weaker inches away or flips him altogether upside down. Almost all combats, however, stop short of a violent finish.

The work described below shows that most combats are so fully ritualized that the observer can detect no element of force. In these encounters the end activity is the rubbing or tapping of a correlated structure by a different part of the opponent's claw. Morphological specializations include ridges, tubercles, and other structures.

At times the effective meeting of parts seems to be achieved through cooperative movements of the less active crab. In the most elaborate combats the components are performed by each individual in turn, while his partner holds still.

Preliminary observations on ritualized combat in *Uca* were made in the Indo-Pacific (Crane, 1966). In some species the claws, partly engaged, vibrated back and forth with a clicking sound audible to the observer. Detailed descriptions were not secured in the field, although motion pictures recorded the pattern. In other forms, pits and tubercles apparently served as deterrents to forceful linkage of the chelipeds. These observations, made incidentally during a study of waving display, all showed the need for a concentrated study of combat.

Such field work was accordingly undertaken in Trinidad during 1966. A socially advanced neotropical species, *rapax*, was selected as the principal subject; comparative observations on other species have begun. The results give some basic information on the occurrence and organization of combat. In this section are also included data on the results of a group of individual combats. Discussions of the functions and origins of combat are reserved, as for other social components described in this chapter, for later consideration. Since then field work on combat has continued in the northeastern United States, in New Guinea, and in Ceylon.

II. *Historical Review*

The fighting proclivities of male fiddler crabs have long been familiar to naturalists strolling on suitable shores. Compared with other conspicuous fiddler activities, however, combats are so uncommon, short, fast, and superficially similar that it is not entirely surprising that their patterned complexities have been overlooked. The infrequent reports were only roughly descriptive and wholly unanalytical. Examples include Pearse (1912.2); Dembowski (1925); Verwey (1930); Crane (1941.1, 1958, 1966).

Intermale combat in other brachyurans occasionally has been reported. Observations have been made on ocypodids, in addition to *Uca*, as follows: in *Dotilla* by Tweedie (1950.3) and Altevogt (1957.2); in *Heloecius* by Tweedie (1954) and Griffin (1968); in *Ocypode quadrata* by Schöne (1968). I have seen combats, but not hitherto reported them, in *Dotilla* and *Heloecius*, as well as in *Scopimera*, *Macrophthalmus*, and *Ilyplax*. Schöne's contribution consists of an illustrated survey of agonistic and sexual display in a wide variety of brachyuran crabs, both aquatic and semi-terrestrial; his list of references is comprehensive. His application of the adjectives "wild" and "irregular" to fighting without apparently formal patterns corresponds to part of the usage of "forceful fighting" in the present contribution; he reports its occurrence in one or more species in the families Cancridae, Portunidae, Xanthidae, Majidae, Parthenopidae, and Grapsidae, as well as in Ocypodidae.

He reports mutual pushing with the chelipeds in a more formal pattern in *Ocypode quadrata*, a member of the genus most closely related to *Uca*. After an account of its threat display Schöne continues, "The most common type of fight is a formalized interaction. The threatening crabs raise themselves higher, lift the first walking legs, close up, touch the fronts of the chelae, and push. After the push, which can be very short, they part, and one or both walk away. Wild attacks have rarely been observed."

Schöne observed similar behavior in two spider crabs, *Maja verrucosa* and *Euryneme aspera*. Of the first species Schöne writes as follows:

> In the irregular fight of *Maja verrucosa*, the opponents thrust and strike with chelae and first walking legs. Often one seizes the other crab's legs and twists. This sometimes leads to loss of a leg in the smaller animal. A formalized type of fight has been observed between males, especially when the male defends the female during the mating period. The male turns against the approaching crab, raises the chelipeds to low-intensity threat, and sometimes strikes. Both crabs close to touching distance and extend the chelipeds to the sides. Each one tries to adjust the chelipeds so that they touch those of the opponent over the whole length. This may last for several seconds. Often the pincers hold each other. Then the crabs press and shift the chelipeds forwards-upwards. The fight continues in the irregular manner as described above.

Additionally, Griffin (1968) has described the combat of the grapsoid *Hemiplax latifrons* and Warner (1970) of the grapsids *Aratus pisoni* and *Goniopsis cruentata*.

None of these examples of relatively regular pushing procedures, although they are formal in comparison with irregular and wild fighting, attain either the ceremonial character or the complexity of high-intensity "ritualized combat" in the sense used in the following pages.

Although the study of acoustical behavior in *Uca* is now progressing (ref.: pp. 480ff), the sounds of combat have yet to be recorded; occasionally they are audible to man. A review by Guinot-Dumortier & Dumortier (1960) on the morphology of stridulation in crabs gives no examples where one crab is presumed to stridulate against another part of another individual.

References to the concept of ritualization in animals are given in the next chapter (p. 519). Ritualized combat is specifically discussed by Lorenz (1964, 1966.1, 1966.2).

Temporary physiological conditions termed phases (Crane, 1958), important in combat, are described on pages 505 and 687.

III. *Organization of Combat in* Uca

(*a*) RELEVANT CHARACTERISTICS OF OPPONENTS IN *U. rapax*

The pattern of a combat between *rapax* males depends largely on three factors: the phase of each individual; the relative size of the two crabs; and the location—whether on the right or left side—of the large claw of each.

Phase. Males engage in combat only when they are in either the aggressive wandering phase or the waving display phase. In the latter condition they are always burrow-holders. Combats take place only between an aggressive wanderer and a burrow-holder or between two burrow-holders; encounters between two aggressive wanderers are unknown. When a wanderer elicits combat from a burrow-holder irregular components are frequent and a ritualized encounter sometimes ends as a forceful fight. In contrast, combats between neighboring males are usually composed of highly regular, ritualized components and practically never end in force. These categories and their results will be described beginning on p. 492.

Relative Size. The larger crab in all combats usually has the advantage. It is interesting, therefore, that, in the majority of combats including an aggressive wanderer, the latter instigates combat with a burrow-holder larger than he.

Claw of Same or Opposite Side Enlarged. In *rapax* as usual in *Uca* (p. 451) right- and left-clawed individuals occur in equal numbers. In the total count given in Table 15, no tendency is shown in combat for instigators to approach opponents having the same claw enlarged as their own rather than the claw on the opposite side. Therefore, homoclawed and heteroclawed combats are about equally likely to take place. Table 16 shows clearly that the frequency of several of the components described below is affected by this characteristic.

(*b*) COMPONENTS OF COMBAT

In the earlier account of combat five separate ritualized components were recorded, only one of which, the heel-and-hollow, was not observed in Trinidad *rapax*. This number has now been increased to 15, through field observations on *pugnax* (subgenus *Minuca*) and, in the subgenus *Celuca*, *pugilator* and *lactea*.

In fiddler crabs many combats can be clearly divided between those that are forceful and those in which pushing and gripping are absent. Other combats obviously include both forceful and non-forceful components. In still others, particularly when the outer surfaces of the two mani are in contact, it is often impossible to determine whether or not force is involved.

The components first described below will be the basic, forceful elements of unritualized fights. Their distribution appears to be genus-wide. In addition to their use of obviously strong pressures of various kinds, they are distinguished by variations in the form of the shoves and seizures as well as by the unpredictability of their sequences. They are not included in Table 14.

The second group includes the 15 types of action now considered to be distinct, non-forceful components of ritualized combat. Since the earlier paper another component, there termed "taps," has been included as a part of each of the several other components in which it sometimes forms a climax. Separate paragraphs will, in addition, be devoted to it at the end of the descriptions of the regular components.

In any ritualized combat the components are very rarely or never performed simultaneously by both crabs. The temporarily active crab is here termed the "actor" and his inactive opponent the "inactor." Parts of the claw of the actor serve as the "instrument" for the performance of each component, while correlated parts of the inactor's claw form the "friction area." As shown in Table 14, each component involves the direct use of from three to twelve or more structures, almost always different, by both actor and inactor.

(*c*) FORCEFUL COMPONENTS

1. *Manus-push.* The chelipeds are held flexed, the chelae partly open through slight lifting of the dactyls. Meanwhile the lower, smoother halves of the mani are pushed against each other. It is often impossible to decide whether or not a manus-push includes a rub component or vice versa. (Pl. 45 *A*.)

2. *Grips, Flings, and Upsets.* The occasional forceful end of a combat is composed of irregular elements that appear to be largely or wholly unritualized. They may be grouped under grips, flings, and upsets—descriptive terms for actions that merge into one another. (Pl. 45 *B*.)

A grip occasionally follows an unsuccessful attempt by an aggressive wanderer to get into the heel-and-ridge position; the fingers then slip beyond the normal position and firmly seize the base of the manus with one finger hooked into the carpal cavity; even the carpus itself may be grasped. Sometimes grips occur when two crabs are grossly mismatched in size; then the larger may seize the entire manus of the smaller crosswise between his fingers. More often the forceful component consists only of a longitudinal grip, with perhaps an undetected push, the actor then opening his fingers. Almost always the crabs then separate.

The term "fling" here includes those actions, always starting with a grip, that result in a skid or partial upset of the opponent. The momentum of the actor's pushing grip carries the released crab sliding backward, or he is thrust off balance with some of his ambulatories off the ground. "Upset" is confined to actions resulting in the complete overturn of the opponent onto his carapace, with all of his ambulatories in the air.

Both the occurrence and the progress of these forceful endings have so far proved to be unpredictable. The following figures, gathered in the study on *rapax*, are relevant. In 180 combats in which the endings were adequately observed, 15 (8.3 percent) ended forcefully. In 14 fights the opponents were an aggressive wanderer and a burrow-holder; the wanderer was larger than the burrow-holder in 7 combats, smaller in 6, while his identity was uncertain in 1; homoclawed and heteroclawed combats were equally divided. In 6 fights the forceful component consisted of a grip only, 5 others ended in flings, and only 3 in total upsets. The burrow-holder was the actor both during the preceding ritualized component and in the grip and subsequent action in 7 combats, the aggressive wander in 2, 1 of them resulting in the eviction of the burrow-holder; in 2 fights both ritualized and force components were mutual, 1 of them resulting in the second observed eviction of a burrow-holder; in 1 fight the action consisted wholly in the eviction of an aggressive wanderer that had slipped in while the burrow-holder was engaged with a neighbor. The ritualized components immediately preceding forceful endings were interlaces in 7 fights and well-developed heel-and-ridges with taps in 3; antecedents to the grip in the remaining examples were irregular or improperly observed. Finally, 5 fights were followed by reduced aggressiveness of the wanderer and 2 by the dispossession of a burrow-holder by a wanderer.

The single forceful ending to a combat between burrow-holders was very short; the slightly smaller instigator lightly seized the opponent's entire palm, then released it and went home; both crabs promptly resumed waving.

In brief, about 1 in 12 combats had a forceful ending, usually consisting only of a brief grasp by one crab of the other's manus; 14 out of 15 fights were between an aggressive wanderer and a burrow-holder; in most the burrow-holder was the active crab at the end of the fight, seizing the wanderer and administering the final push, fling, or upset. Forceful components preceded reductions in the wanderer's aggressiveness in 5 combats and preceded the taking over of his opponent's burrow in 2. These changes in behavior will be further discussed beginning on p. 493 and are included in Table 18.

(*d*) RITUALIZED COMPONENTS

In the first two components below, only the outer surfaces of the claw come into contact; they are viewed as constituting the low-intensity components of combat behavior. In the remaining components, a part of each claw enters the gape of the opponent and they are all considered to be of high intensity.

1. *Manus-rub* (Fig. 39). The outer sides of the opposing mani are rubbed back and forth, longitudinally, against each other. In most species the lower halves are nearly smooth and it is there that the surfaces usually come into contact. It is possible that the rubbing over the smooth surface facilitates the attainment of high-intensity components. At these times the manus-rub continues past the bases of the gapes until the chelae are in contact externally and are free to proceed to one or more of the following components. Tapping very rarely follows the rubbing; when it does so it is as distinct as in the components where it often occurs.

2. *Pollex-rub.* An extension of the manus-rub, in which the outer sides of the pollices rub longitudinally. On the outer propodus *U. pugilator* has a low keel with an adjacent groove beside its upper edge. Starting on the lower distal part of the manus, the keel and groove continue out along the lower side of the pollex, well above the ventral margin. During both the manus-rub and the pollex-rub *pugilator* tilts the lower half of the propodus outward. In this way, the smoothest parts of the opposing mani and the full lengths of the keels are clearly concerned in the rubbing.

3. *Pollex-under-and-over-slide.* The actor rubs the prehensile edge of his pollex along the ventral mar-

gin of his opponent's pollex, from near its distal end to a point ranging from near the pollex base to slightly beyond it, on the lower edge of the manus. The actor then momentarily disengages. Without a pause he promptly slides the ventral edge of his own pollex along the prehensile edge of that of his opponent.

4. *Subdactyl-and-subpollex-slide.* The actor slides the dorsal edge of his dactyl along the prehensile edge of his opponent's dactyl while, simultaneously, he also slides the prehensile edge of his pollex along the ventral margin of the opponent's pollex. Single points on the proximal half of the actor's dactyl and pollex form the instruments, but the slide may be along the full length of the opponent's chela.

5. *Pollex-base-rub.* (In each of the several examples seen of this component a burrow-holder was partly down his burrow, with his flexed major cheliped still visible, the mano-carpal joint highest, but the pollex and dactyl still exposed, their tips touching the ground. The encounters were all heteroclawed.) The actor approaches the burrow-holder, the cheliped being slightly flexed and the upper part of the manus and the dactyl being tilted toward the inside. In this position the actor's pollex is at a convenient height to reach through the burrow-holder's gape, from its inner side. The pollex then, with the tubercles of the middle region of its prehensile edge, rubs vertically up and down. The contact area is the flat area at the base of the burrow-holder's pollex. The motion in the examples seen was repeated in several short series of two or three up-and-down motions each.

6. *Dactyl-slide* (Fig. 86 *A*). With the chelae of both crabs partly open, the dactyl of one moves on top of that of the opponent at about the middle of its length, more or less at right angles, while the pollex passes within the gape. The approach may be from either the inner or the outer side of the claw. Both chelae are by then widely opened and the pollex does not touch the opponent's fingers. Gentle maneuvering for this position may continue for several seconds. Once it is achieved, the rounded teeth of the actor's dactyl slide longitudinally back and forth along the middle portion of the upper edge of the opponent's dactyl. No force seems to be used by either crab and no attempt is made to use the claws as pincers, all four tips being at all times free in the air. Except for the sliding motion both crabs remain almost motionless. An infrequent climax is the vibratory tapping of the uppermost dactyl against the one held quietly beneath it. In *rapax*, at least, the vibration is performed only by the crab with the dactyl on top. Afterward the two crabs break suddenly apart. When tapping does not occur, the encounter either breaks off after at most several seconds of slide or, infrequently, passes into component 9 or 12 below. Dactyl slides occur more often in heteroclawed than in homoclawed combat.

7. *Upper-and-lower-manus-rub.* In a commonly occurring forceful grip, the actor seizes the opponent's entire manus between the prehensile edges of his dactyl and pollex. In this fully ritualized version, designated component 7, the initial position is identical, but no pressure whatever appears to be used. Instead, the actor rubs the prehensile edges of his claw longitudinally back and forth at least along the dorsal and ventral margins of the manus and sometimes also continuing distally onto the corresponding margins of dactyl and pollex. The timing is relatively slow and tapping has not been seen. In the earlier account of combat (Crane, 1967), this ritualized component was not differentiated from its forceful version, which was included without special comment among the grips, flings, and upsets. Since I became aware of this highly ritualized form through observaitons of *pugnax*, *pugilator*, and *lactea*, a review of the early notes and films of *rapax* has shown that it occurs in that species too. At the time I considered it only one more example of indeterminate, irregular behavior by aggressive wanderers.

8. *Dactyl-submanus-slide.* The burrow-holder is partway down his burrow, with the flexed cheliped obliquely raised, about as in component 5, the ventral edge of the manus being clear of the ground. Only three encounters are known, all homoclawed. The opponent-to-be, the actor, approaches with his cheliped flexed and the mano-carpal joint similarly raised, as in threat component 1. The actor then gently slides the prehensile edge of his dactyl along the ventral margin of the manus of the burrow-holder, the longitudinal rub being repeated once or twice. The actor then stops. The burrow-holder promptly emerges and, reversing roles with his opponent, repeats the motions. The former actor has meanwhile tilted his manus so that its lower edge is more accessible to the dactyl of the burrow-holder. With both crabs now on the surface, the necessary postures appeared awkward for both, but they did not hesitate in any of the observed encounters. In each the burrow-holder made a number of rather slow slides. Then the original actor went away. The terms "instigator" and "aggressive wanderer" are not used, since in the northern species in which the component was observed the social situations were not clearly evident.

9. *Interlace* (Figs. 86 *D*, *E*; Pl. 45 *E*, *F*). In this component the fingers of each claw overlap the opponent's manus, so that the bases of the gapes are almost or wholly in contact. The sequence is charac-

teristic of heteroclawed combats although not confined to them. Typically the position is assumed by the crab that has its dactyl against the inner side of the opponent's manus rather than against the outer side, which is the position for a heel-and-ridge (component 12). In a fully developed interlace the chela of each crab is wide open through high elevation of the dactyl; the tips of both pollex and dactyl are wholly free from contact with any part of the opponent. In this position the most proximal teeth of the pollex come into contact with one or both of the tuberculated ridges paralleling the base of the opponent's dactyl and rub up and down along their course. At highest intensity the rub follows along the longer, less variable subdistal ridge that continues from the dactyl base down around the base of the gape and out along the proximal, upper, inner portion of the pollex.

The climax usually consists of frication by the pollex teeth as just described, whereupon the encounter ends. This component may culminate in serial taps similar to those following a normal heel-and-ridge component but made, instead, by the basal gape teeth against the subdistal ridge of the manus in the interlace position. While a tapping finale is the normal end of a fully developed heel-and-ridge component, it is uncommon after an interlace and, as when it follows a dactyl slide, cannot be regarded as typical (p. 491).

An interlace is usually preceded by a manus-rub and less often by a dactyl-slide. It also occurs in mutual heteroclawed encounters when one opponent, with the dactyl against the inner side of the other's manus, performs the interlace. Usually it is the temporarily more active crab, in passing from a low-intensity manus-rub to high-intensity, that assumes the heel-and-ridge position, with the dactyl outside the manus; hence the second crab arrives automatically in a position appropriate for the interlace.

10. *Pregape-rub.* This component occurs more often in homoclawed than in heteroclawed encounters, as does the heel-and-ridge (component 12). The positions are similar in both, the chelae being partly linked with the dactyl of the actor in contact with the outer manus of his opponent, while his own pollex lies against the opponent's palm. In the pregape-rub, however, both friction areas are near the base of the gape, while the movement is longitudinal, not vertical or oblique. The tips of the chela seem chiefly to be used in the rub, which has been observed clearly only three times, in *pugilator* only. Its unritualized counterpart is a grip, with the point of seizure in the same position, that occurs frequently in the genus.

11. *Heel-and-hollow.* This component is known only in Indo-Pacific species. The degree of ritualization it attains apparently varies with the subgenus. Force is sometimes clearly involved, yet at least in *lactea* (subgenus *Celuca*) highly ritualized tapping sometimes forms the entire component. In the component, the tip of the pollex is inserted in or does not pass beyond the hollow near the pollex base. The dactyl holds a position similar to that in the pregape rub or as in *lactea*, the heel-and-ridge (components 10 and 12), since it lies against the outer manus.

12. *Heel-and-ridge* (Figs. 86 *B*, *C*; Pl. 45 *C*, *D*). In *rapax* and many other species the dactyl, longer than the pollex, curves downward beyond it. This characteristic proves to be of definite use in heel-and-ridging, where the dactyl arches around the curving heel outside the manus of the opponent. On its way toward the heel, the dactyl tip appears to feel its way, using as a guide the outer crease along the base of the dorsal marginal ridge. Afterward, upon reaching the proximal part of the manus, the dactyl tip does not touch the heel except during the climax to be described. Meanwhile the pollex, shorter than the dactyl and virtually straight, comes into contact with the oblique tuberculated ridge of the inner manus. The pollex teeth, in the examples where an adequate view or film was secured, rub up and down along the oblique ridge. At the climax, however, the actor taps the ridge rapidly three or four times with his pollex; on opposite strokes, when the pollex is away from the ridge, the teeth near the dactyl tip come into contact with the manus heel. At highest intensity the tapping is faster and of smaller amplitude; the effect is vibratory (p. 491). It is always the actor of the moment—not necessarily by now the original instigator—that performs the tapping. No attempt at seizing and gripping has ever been detected when the claws are in the heel-and-ridge position. In *rapax* a heel-and-ridge may be preceded by a manus-rub or infrequently by a dactyl-slide. Occasionally in mutual, heteroclawed combat a heel-and-ridge is followed by or alternates with an interlace.

13. *Supraheel-rub.* The actor places his dactyl around the outside of the manus, the pollex against the palm, about as in the heel-and-ridge (component 12). The position of the dactyl is however higher, against the upper, proximal part of the other's manus. Here the distal part of the actor's dactyl makes rapid, up-and-down rubs, different in direction as well as position from those occurring in a heel-and-ridge. In each of the few examples seen the position and motion of the pollex was invisible. It is possible that the positions assumed by the dactyl on the outer manus in the pregape-rub and supraheel-rub (components 10 and 13) are associated with the vestigial development of the oblique ridge on the palm in *pugilator*, along with its characteristic tuberculation, which may well be involved in the positions of the dactyl as well as of the more directly concerned pollex.

14. *Dactyl-along-pollex-groove.* The actor places the distal part of the prehensile edge of his dactyl against the groove in the proximal part of the inactor's outer pollex, and rubs back and forth along the groove; sometimes the rubbing continues into the hollow at the distal end of the manus. This component, only rarely observed, occurs in both homoclawed and heteroclawed combat. The position is obviously more easily attained in heteroclawed combats; when homoclawed opponents perform it, the actor tilts his claw appropriately.

15. *Subdactyl-and-suprapollex-saw.* With the median and distal part of his dactyl's prehensile edge, the actor rubs at right angles across the distal half of the prehensile edge of the inactor's pollex, between the two large projections that often occur on the pollex in *vocans*, the only species yet known to perform this component.

(*e*) TAPPING

In threat and courtship behavior a number of species make drumming motions of chelipeds or legs against the ground, their own carapaces, or both. These motions all appear to form separate components. In combat, on the other hand, a similar motion now and then climaxes five different components, and is always preceded by one of them, the tapping occurring without a change of position immediately after the characteristic form of rubbing. It seems appropriate, therefore, not to give tapping the rank of a component. The five components it is known to follow are the manus-rub, dactyl-slide, interlace, heel-and-hollow, and heel-and-ridge (numbers 1, 6, 9, 11 and 12).

An exceptional form of tapping occurs in recently studied populations of *lactea.* Here, tapping of the outer surfaces of the mani does not necessarily follow closely on any component, and often in fact inaugurates the encounter, or forms the only part of it. It is, in fact, elaborated and intensified to such a degree that it must be viewed as a separate component. In a subsequent contribution, now in preparation, it will be termed *clacking.*

The following details of the more usual form of tapping were all assembled during the study of *rapax* in Trinidad. In this species tapping occurs most frequently at the end of a heel-and-ridge component. Sometimes it is preceded by an interlace or dactyl-slide; rarely by a manus-rub. Always it consists of the rapid tapping of the dactyl or, in most heel-and-ridge sequences, of the dactyl and pollex alternately, against a particular part of the opponent's claw. Rather slow tapping of wide amplitude is performed both by aggressive wanderers and by burrow-holders. Rapid taps of narrow amplitude are performed only by a burrow-holder, usually at the end of an encounter beside his own hole. The several examples recorded on motion picture film appear as blurs on frames exposed at 1/48 second. After tapping, a combat often breaks off abruptly.

(*f*) ACTIVITIES ASSOCIATED WITH COMBAT

1. *Withdrawals.* Certain associated activities of combat may be termed withdrawals. In all, a burrow-holder descends partly or wholly underground in the presence of an opponent, whether potential or actual. He may either refuse to respond at all to the initial threat of an approaching male, or he may withdraw in the midst of a combat, even when he has the advantage of size. The reasons for these withdrawals of larger males are worthy of a separate investigation. Partial withdrawals leaving only part of the chela itself on the surface are exceedingly common throughout the genus, and almost always occur before the trespassing crab comes within reach of the burrow-holder. The various degrees of projection of the chela have already been included among the groups of threat components (p. 479). An aggressive wanderer may or may not make prying motions at the claw with his own chela (Fig. 84 *D*) or ambulatories, or may even stamp on a flat claw before passing on. The flat-clawed partial withdrawals appear very rarely if at all to occur in encounters between neighboring burrow-holders, and seem most often to be prevalent in crowded populations with plentiful aggressive wanderers. Counts and distance measurements have still to be begun. Withdrawal wholly underground almost always occurs when the crab's opponent, whether an aggressive wanderer or a trespassing male from another burrow, is larger than he. Very rarely an opponent tries to dig out the burrow-holder that has withdrawn from an actual combat.

A second class of withdrawals exists which perhaps should be differentiated and termed false-withdrawals, although they sometimes are followed by total withdrawal. A false-withdrawal is always partial and only apparent, since the burrow-holder clearly uses the upper part of his burrow as a firm foothold for the prosecution of a combat. Three recently identified components, the pollex base-rub, dactyl-submanus-slide, and supraheel-rub (numbers 5, 8, and 13) in the examples seen have almost always at least begun when a burrow-holder has partly descended, leaving most of the flexed cheliped thrusting vertically into the air. In addition, I have seen these half-withdrawn burrow-holders engage most effectively in all classes of combat, both forceful and ritualized.

2. *Down-pushes.* This forceful form of behavior has been seen in a number of species, but was observed in detail only four times, all ending combats in *rapax.* In each of these a crab actively pushed his opponent

down the latter's own burrow. Three of the combats were between burrow-holders, the actor using the low-intensity manus-push. In one of these the instigator was the smaller crab; the larger pushed him back to his own burrow, alternating manus-pushes with manus-rubs. The fourth down-push marked the end of a meeting between an aggressive wanderer and a burrow-holder; the down-push was the only noteworthy part of the brief combat, which included a manus-rub and an irregular interlace. In this fight the down-push was delivered by a final grip.

3. *After-lunges.* The after-lunge is included among the threat components (p. 479) since it appears to be identical with the usual lunge of pure threat behavior. It often follows combat, apparently throughout the genus; in *rapax* after-lunges were counted in almost half the combats in which its presence or absence was noted. Sometimes it follows a combat so closely that perhaps it should then be considered a component. Such distinctions between after-lunges, however, would be too blurred to be practical.

4. *Removal of Burrow Intruders.* This behavior has frequently been seen in a number of species. It usually occurs when a smaller crab slips unnoticed down the hole while the burrow-holder is engaged in combat. The returning crab then digs up the intruder, or, when the latter is small enough, thrusts his major cheliped down the hole and flips the little one out. The motions used are also found under certain conditions among crabs not in display phase but seeking burrows for shelter from the tide (p. 511).

(*g*) CATEGORIES

This section is used practically unchanged from the previous contribution on combat (*loc. cit.*, pp. 62-63). Although the figures included are all derived from the detailed study of *U. rapax* in Trinidad, the general statements appear to be widely applicable to the organization of combats in a number of other species.

The preceding accounts of behavior components have mentioned two general classes of combats, those between an aggressive wanderer and a burrow-holder and those between two burrow-holders. The characteristics of each will now be considered as a basis for a review of combat results. Mutual combat occurs in both categories but will be examined more closely under subheading 3 below.

1. *Combats between an Aggressive Wanderer and a Burrow-Holder.* These combats are notable for their irregularity, for the prevalence of forceful grips, and for the frequent withdrawal of a vigorous burrow-holder from an encounter. In first determining the combat repertory of any species of *Uca*, in fact, it is misleading to concentrate on combats involving aggressive wanderers. Such descriptions might easily be as inaccurate as reports on the nest-building behavior of birds drawn from observations of individuals that have not fully reached breeding condition.

Unfortunately for the observer, the combat activities of fiddler crabs in this phase are often more numerous and certainly more easily foreseen than are encounters between burrow-holders. It is temptingly convenient to select for attention an active aggressive wanderer and watch him on his progress through the population. Such a course is usually conveniently marked by the threats of burrow-holders on his route. If his aggressive phase is well established, a number of combats may be thus observed. Once the repertory of a species is partially known, of course, the combats instigated by these wanderers form a rich source of information.

The combats may be composed of one or most of the components previously described. Often, however, the high-intensity components—dactyl-slides, heel-and-ridges, and interlaces—are imperfectly attained or the motions are atypical; tapping, if any, is of wide amplitude.

For example, several aggressive wanderers, after an uneventful manus-rub, inserted both pollex and dactyl through the gape of the burrow-holder's chela, instead of inserting only the pollex. No regular combat development by the wanderer seemed possible from this position. One such contest ended with the burrow-holder's opening his chela wide and freeing himself. In another the crabs broke apart after awkward shaking and shoving. After each of these encounters the wanderer departed.

Similarly, an apparently clumsy attempt is sometimes made by the wanderer to attain a dorsal-slide position. This the opponent thwarts by raising his own dactyl high. The maneuver does not happen in fully ritualized fights between burrow-holders, when the opponent usually appears wholly unresisting and—one is tempted to say—cooperative. When a slide position is obtained, the wanderer sometimes saws back and forth transversely across a single spot on the opponent's upper dactyl rather than in the normal longitudinal direction.

The behavior of a burrow-holder approached by an aggressive wanderer is often atypical of his normally aggressive display phase; this is true even when, as is usually the case, the wanderer is the smaller crab. As described under Withdrawals (p. 491), the burrow-holder sometimes goes partly or completely underground either when approached or later in the course of the encounter. When the wanderer has passed, the burrow-holder emerges promptly and resumes display.

In a series of 180 combats in *rapax*, all except one of the 15 forceful endings took place at the close of a burrow-holder's fight with an aggressive wanderer.

2. *Combats between Two Burrow-Holders.* These encounters usually occur at the mouth of the burrow of one of the participants. In contrast to the usual procedure in combats started by an aggressive wanderer, the instigator in this category is usually the larger crab. A minority of encounters between burrow-holders take place on or close to the boundary between two territories.

The same two neighboring crabs occasionally proceed through highly ritualized combats a number of times during a single low tide. Sometimes a burrow-holder seems to be attracted to his neighbor's vicinity by a combat between the neighbor and another crab, usually an aggressive wanderer. Irregularities in the performance of the components are rare, combats brief, and forceful endings practically absent.

3. *Mutual Combats.* About one-third of all combats in the *rapax* series were strongly mutual in the sense that each crab performs at least one of the ritualized components. In the 154 combats analyzed in Tables 15 and 16, mutual elements were detected in 38 percent of the combats between an aggressive wanderer and a burrow-holder, and in 31 percent of those between two burrow-holders. In 87 percent of the mutual combats including an aggressive wanderer, the latter was smaller than the burrow-holder he approached; this figure is higher than the proportion (67 percent) of smaller wanderers in the entire combat sample.

In a few additional combats, which are included in Tables 15 and 18, an aggressive wanderer's only activity appeared to be the initial approach to the burrow-holder. After that the burrow-holder seemed to be the sole actor and the wanderer eventually departed. Similar cases were observed twice in combats between burrow-holders. No doubt many more such examples were seen than are cited in the tables; they are not included since the instigator's inactivity, whether he was a wanderer or a neighbor, could be only suspected because the angle of observation was unsatisfactory.

The heart of the problem of instigator inactivity lies in the observation of low-intensity components, the manus-rubs. The actor or actors are especially difficult to detect, even in motion picture close-ups, because manus-rubbing is the only component in which mutual action can be performed simultaneously by both crabs; this of course is because the necessary juxtaposition of parts—outer manus to outer manus—is much less precise than in the subsequent components of high-intensity combat. Even in the analyses of highly mutual combats, the counts for mutual manus-rubs are doubtless low; when uncertain about the mutuality of a rub, I counted it as absent.

In ritualized components of high intensity—dactyl-slides, heel-and-ridges, and interlaces—the actors either perform the slide in turn or exchange roles, the former actor holding still while the second crab performs the next component. Any necessary shift in position is made, including those demanded by a different size of claw. Sometimes the temporarily inactive crab is not only quiescent during and after the shift but even appears to take a cooperative part in it. For example, after a slide a retiring actor brought his dactyl below that of his opponent, into the latter's gape, and then stopped moving. This left the other crab in the actor's position for the slide that promptly followed.

In mutual heteroclawed combats the heel-and-ridge is performed by the individual's having his dactyl outside the manus, the interlace by the crab with the dactyl against the inner surface, as described on p. 490. When the second crab becomes the actor, he needs only to engage the claws farther, to the gape base, to attain fully the interlace position.

A total of 11 heteroclawed combats were observed in the *rapax* series which included this alternate performance of heel-and-ridging with interlacing; one record was secured on motion picture film; all except one of these examples took place between an aggressive wanderer and a burrow-holder.

Although some mutual encounters were among the best examples of ritualized combat, with no discernible trace of force, in others aggressive elements were scarcely disguised. In these combats the shift from one actor to another was clearly accompanied by irregular pushing or by abruptly jerking motions of a claw in the midst of a component.

(*h*) DURATION

The duration of a group of combats has been investigated only in *rapax*. Here 104 combats, of all classes, each observed from its beginning, were approximately timed. The great majority turned out to be very short encounters, most of them lasting between about 3 and 8 seconds, and all but 9 lasting less than 20 seconds. Each of these 9 continued for more than a minute and included high-intensity components. Proportionately more of these long combats occurred between right- and left-clawed crabs, more had mutual components and more ended forcefully than did short combats.

IV. *Post-Combat Behavior*

After most encounters between *rapax* males, the opponents promptly resumed their pre-combat activity. Aggressive wanderers passed on through the population, instigating new combats and engaging in other activities (pp. 487, 492, 505, and 687). Burrow-holders, returning with equal completeness to all their former activities, first resumed waving. Similar sequels to combat have now been observed in a number of other species.

Almost one quarter of all encounters in *rapax* which were sufficiently observed, however, were followed by detectable changes in behavior. In all the combats of the series, both opponents were watched long enough in 148 examples to form a suitable basis for an examination of such changes and of combat composition when subsequent changes did not occur. These alterations in behavior were of two kinds: either the aggressiveness of an aggressive wanderer was reduced or there was an appreciable delay in the resumption of waving by a burrow-holder. Reduction of aggressiveness in a wanderer and delayed waving by the burrow-holder never followed the same combat, nor was waving ever delayed by both opposing burrow-holders.

Table 18 breaks down the 148 combats where subsequent behavior was observed into a number of potentially relevant subdivisions. The first column, headed Result, divides the group into those with behavior unchanged, waving delayed, or aggression reduced. In the second column, Combat Class, the opponents' phases and relative size are indicated, as in previous tables, as well as, where necessary, the instigator and the site of the combat. Under General Combat Composition selected characteristics are isolated; these show the relative prevalence of low- and high-intensity combats, forceful components, tapping, and mutual components. It seemed that one or more of these aspects of combat might be correlated with behavior changes or the lack of them. However, no clear-cut correlation emerges. For example, neither tapping nor mutual components preclude either a delay in resumption of waving or reduced aggression; similarly, forceful endings are not necessarily followed by subsequent behavior changes. Nevertheless, certain trends are indicated.

Five points emerge that seem noteworthy in spite of the small samples. First, in combats followed by the reduced aggressiveness of a wanderer, forceful endings were more numerous than in combats either not followed by behavior changes or with a subsequent delay in resumption of waving. Second, long combats were most numerous in the class followed by delayed waving, less so among those resulting in reduced aggression, and rare among encounters with no detectable results. Third, mutual components were relatively fewer in combats followed by changes in behavior. Fourth, tapping was usually absent from encounters with forceful endings; this absence is probably correlated with the frequently prompt cessation of combat after tapping. When tapping did occur in the course of a fight ending forcefully, subsequent behavior was changed. Finally, after combat any changes in behavior were usually shown by the smaller crab.

Since the study of combat in *rapax* was made entirely in the field among unmarked crabs, few hints of summation were observed. When this important aspect is suitably investigated, summation will almost certainly prove to play a part in the effects of combat.

A study comparable to the investigation of *rapax* is in preparation on combat in (*Celuca*) *lactea.* The most striking difference between the two species is the relative incidence of force. Whereas in the *rapax* series only 9 percent of high-intensity combats ended forcefully, in *lactea* the percentage ranged from 48 to 65. Again, after the rare forceful ending in *rapax* combats the final inactor seemed never to return for another engagement; in *lactea*, on the other hand, the same individual often picked himself up after an upset and came back promptly for one or more additional rounds. Each of the subsequent fights often ended in a fashion similar to the first. As in *rapax*, occupancy of a burrow was not an immediate aim. Finally, in *lactea*, the equivalent of manus-rubs or -taps was a strongly forceful component that was almost always a major element (p. 491). Yet both the positions and motions were so stereotyped and of such an exaggerated nature that they appeared as ritualized as any of the complex components known in other species. Thus force itself has been ritualized, and my early definition of a ritualized combat or component in *Uca* as one in which force plays no apparent part breaks down. To cover the changed situation, I am now substituting a more satisfactory phrase. For the purposes of this contribution, ritualized combats or components lack the ingredient of irregular force.

F. WAVING DISPLAY

I. *Introduction*

As the exaggerated size of one cheliped is the most typical morphological characteristic in fiddler crabs, so the "waving" of this appendage in visual display is unique among appendages in the variety and complexity of its patterns of movement.

In this contribution, the term *waving display* is used in a general sense to include not only the motions of the major cheliped, but all other movements associated with the waving category of apparently visual display. Equivocal displays that may include sound components, although they are mentioned below, will be discussed in more detail in the next chapter.

II. *Historical Review*

Rhythmic motions of both chelipeds have been reported in a number of other ocypodids. Those of *Dotilla* were described by Tweedie (1950.3) and Altevogt (1957.2); *Macrophthalmus* and *Ilyoplax* by

Tweedie (1954); and *Heloecius* by Ward (1928), Tweedie (1954), and Griffin (1968). I have also observed waving display in all these genera as well as in *Scopimera* (Crane, unpublished). In some of these forms the carapace is raised and lowered, adding to the conspicuousness of the behavior. In all, the "waving" consists of a relatively simple elevation and extension of the chelipeds, usually up and out, with a return to the rest position. In none are the entire body and a number of appendages also conspicuously involved, nor are the patterns of display as different interspecifically as among the various forms of *Uca*. Roughly similar motions are also known in a number of other grapsoids; pertinent contributions include Tweedie (1954), Schöne (1961, 1968), Schöne & Schöne (1963), Reese (1964), Salmon & Atsaides (1968.2), Wright (1968) and Warner (1969, 1970), along with their respective references.

The first author to mention waving behavior in *Uca* was Rumphius, whose account of East Indian fiddlers was published in 1705. He wrote, "... during ebb tide one sees it strenuously waving the largest claw continuously, as if it wanted to call people, and when one approaches it, it hides in the sand. Its name in Latin is *Cancer Vocans* and in Malayan, Cattam Pangel, that is, the Caller. . . ." Although Linnaeus (1758) adopted the Latin form as an official binomial, and the common names "fiddler-crab" and "winkerkrabbe" came into use (e.g. Smith, 1870.2, Müller, 1881), waving itself seems to have been ignored in print for decades.

Finally came the observations of Alcock (1892, 1902) and Pearse (1912.2, 1914.1, 1914.2), the principal early contributors, who regarded waving, along with colors, as a means of attracting the female. Pearse's 1912 paper, however, noted that fiddlers in the Philippines sometimes waved when no female was present, and in the non-breeding season at that. Starting about the same time, brief remarks on waving, also with the emphasis on the courting character of the display, were contributed by Schwartz & Safir (1915), Symons (1920), Johnson & Snook (1927), Beebe (1928), and Matthews (1930); all of these references except the first noted that males waved more rapidly when a female appeared, as did the more detailed contributions of Crane (1941.1ff.), Burkenroad (1947), von Hagen (1961, 1962), and Salmon & Stout (1962). Altevogt (1955.1, 1955.2, 1957.1, 1959) also favored the courtship interpretation of waving, while the recent work of Salmon (1965, 1967) and of Salmon & Atsaides (1968.2), in the sections where it concerns waving, has concentrated on its relation to courtship. Meanwhile, several other observers decided that the primary, and probably the only, function of waving was to delimit territory; this view was held by Verwey (1930), Hediger (1933.2, 1934), and Gray (1942). To Crane (1941.1, 1957, 1966) and to Schöne & Schöne (1963) waving appeared ambivalent; a similar view will be expanded later (pp. 501, 517).

The history of the descriptions of particular kinds of waving display is shorter. Crane (1941.1, 1943.2, 1943.3) reported specific distinctions in the movements, and attempted descriptions indicating phylogenetic relationships among species in the eastern Pacific, along with a few from the western Atlantic. Since the early accounts of waving, descriptions have become more precise, with the relation of the waving to sound production receiving increasing attention. Burkenroad (1947) discussed correlations between waving and sound production in *pugilator*. Altevogt (1955.1, 1955.2, 1957.2, 1962), Peters (1955), von Hagen (1962, 1968.2), Salmon & Stout (1962), Salmon (1965, 1967), and Salmon & Atsaides (1968.1, 1968.2) have all described visual display in many species in detail, securing data on timing and its variation and on directions of movement through analyses of films.

Crane (1957, 1966), also aided by films, reported a rough division of types of visual display into two categories, termed vertical and lateral waves, each of which was associated with a particular form of daytime courtship. Among species characterized by vertical waves, the male pursues the female toward her burrow, with or without waving; copulation takes place on the surface of the ground; this behavior is characteristic of most species in the Indo-Pacific. Among lateral wavers, on the other hand, the male in normal diurnal courtship attracts the female down his own burrow, which he enters first; this sequence Crane reported to be most characteristic of American species. Intermediate types of display, to be further discussed below, were stated to occur, a circumstance also reported by Salmon (1967), Salmon & Atsaides (1968.2), and von Hagen (1968.2). Recent work, as will be seen, has uncovered further complexities.

Wright (1968), in a comparative study of visual display in semi-terrestrial crabs, observed that waving displays in *Uca*, in spite of their variety, all fit into his general category of Lateral Merus Displays, but that the subdivisions he has distinguished in a number of semi-terrestrial groups are not present. Described here as the Forward-Point (p. 479), Wright's other principal category, the Chela Forward Display, occurs in several species of *Uca*, but only as a threat posture.

The present section is confined to a description of the components, the organization, and the timing of waving display, including its associated motions. In addition, indications are included on the extent of the variations of these displays, both within and among populations.

III. *Components of Waving Display*

(*a*) MOVEMENTS OF MAJOR CHELIPED

1. *Vertical-wave.* The flexed cheliped moves up and down in a single plane in front of the body. In some cases it may strike the ground, then becoming, of course, an example of sound component no. 9 (p. 483). In some Indo-Pacific species the movement forms the entire waving display. (Fig. 90.)

2. *Jerking-vertical-wave.* As in the vertical wave, above, but with definite pauses that appear as jerks. These may be confined to several in the rising period, but usually one or more jerks also occur as the claw is returned to rest position.

3. *Semi-unflexed-wave.* Cheliped partly unflexed during wave, pushing outward and sometimes up to an acute angle with the front. A development of 1 or 2, above, with the jerks largely smoothed out.

4. *Lateral-straight-wave.* The cheliped is completely unflexed, either straight outward or obliquely upward, and returned to the rest position as in 2, in a single plane.

5. *Lateral-circular-wave.* The cheliped is again completely unflexed outward, or obliquely upward, as in 4. Instead of returning to rest position in the same plane, however, the claw is raised, then flexed and brought down to rest position from above the eyes and buccal region. (Fig. 91 *A-D.*) For the only known exception, see *pugilator* (p. 225).

6. *Jerking-oblique-wave.* As in 4 or 5 but with jerks, the initial direction being always obliquely upward, not sometimes straight outward. The jerks range in number from one or two during the unflexing to more than 20; the number on the return descent usually does not exceed several and may be absent. (Fig. 91 *E, F.*)

7. *Reversed-circular-wave.* As in 5, but cheliped is first brought up in front of buccal region, somewhat like the beginning of a vertical wave. After an unflexed high reach, it returns to rest position by being lowered laterally and flexed as it passes parallel to the ground. So far noted only in *pugilator.*

8. *Overhead-circling.* The cheliped does not return to the ground during a series of waves. A development of component 5, it is characteristic of large, heavy crabs in the subgenus *Uca.* Here the motion, found only in high intensity display, is probably an aid to balance. Sometimes occurs in other species when a male is partway down a burrow, with the projecting cheliped continuing to wave.

(*b*) MOVEMENTS OF MINOR CHELIPED

9. *Minor-wave.* The minor cheliped makes a motion similar to that of the major. The small appendage is sometimes almost certainly involved in sound production during some of its motions, but often not at all.

(*c*) MOVEMENTS OF AMBULATORIES

10. *Leg-stretch.* The crab raises its body with each wave, through straightening the leg joints, the crab being supported on the tips of the dactyls. At highest intensity only the two pairs of middle legs, always the longest, touch the ground. The high point of the wave coincides with the greatest elevation of the body. (Fig. 90 *C, D.*)

11. *Prolonged-leg-stretch.* As in 8, except that the position is held throughout a series of waves. (Fig. 90 *E, F.*)

12. *Leg-wave.* This position is closely similar to the acoustical leg-wag (p. 482), two or more legs being raised on a side and moved up and down. Unlike the leg-wag, however, in leg-waving the meri do not touch at all, and the component is purely visual. The raised legs usually reach their highest point at the peak of the major cheliped's elevation, which also coincides with maximum elevation of the body. (Fig. 88 *B, C.*)

13. *Curtsy.* The ambulatories are momentarily depressed, the crab bobbing repeatedly down and up. Depending both on species and circumstances, the curtsy precedes, coincides with, or follows the peak of the wave, or at highest intensity may replace waving.

14. *Herding.* A male stops display, extends the major cheliped laterally, or flexes it above the front, and approaches an attentive female. He then maneuvers her toward his burrow, darting and zigzagging with great agility, while the female just as actively seeks to dodge away from him. Usually he does not touch her until he has chivied her almost to the burrow's edge; if she does not escape, he then sometimes literally pushes her down, following her at once. Sometimes several neighboring males simultaneously attempt to herd a single female.

(*d*) TIMING

15. *Duration of Single Waves.* An important, but highly variable component. Discussed below.

16. *Pause at Peak of Wave.* When present, forms a notable characteristic of the display.

17. *Pause Duration between Waves of a Single Series.* Forms a fairly reliable characteristic only in relation to the tempo of the particular wave series being analyzed.

18. *Number of Waves in Series.* Sometimes a definite and fairly useful characteristic, but not sufficiently well known to include in Table 19.

(*e*) MOTIONS ASSOCIATED WITH WAVING DISPLAY

The preceding list includes only motions or elements of timing that can be expected to add to the visual effect of the waving display; in general they increase the crab's apparent size, make him more conspicuous, or contribute to the distinctiveness of the waving rhythms. There are in addition two general kinds of motions which perhaps also contribute to the visual value of the display; since they belong to other areas of behavior, they are not included either in the annotated list above or in Table 20. These are, first, the motions, sometimes very conspicuous, associated with sound production; a good example is the drumming found in some forms of high intensity courtship. Second are the various kinds of displacement behavior, at times taking visually prominent forms. An example is incomplete drumming motions, where the cheliped touches neither the ground nor, through the merus, the carapace. Some small motions of the minor cheliped, mentioned under visual display component no. 9, above, probably also belong in this anomalous group.

IV. *Organization of Components in Waving Display*

Table 20 gives an idea of the known distribution of components throughout the genus, while Table 19 assembles current data on the timing of the waving part of display. The paragraphs below will comment on this material. Details for each species are given in the systematic section. General discussion is reserved for following chapters.

The clearest examples of relatively simple displays occur in *Deltuca* and *Thalassuca*; here the waves are very low verticals, usually in series, probably with an acoustic drumming component sometimes associated with the downbeat of the cheliped manus. The cheliped is never raised high or stretched out, and during high intensity there are no special kicks, stretches upward, or curtsies. Sometimes the cheliped makes several brief pauses during the raising of the claw, each giving the effect of a jerk; these jerking displays are usually not in series. Sometimes both simple and jerking waves are found in the same display. In one subspecies of *coarctata*, the display of very young crabs consists of jerks, while older individuals give simple waves. Copulation is not always preceded by waving; it occurs at the surface with the male following the female and patting, plucking, or stroking her carapace.

Other Indo-Pacific species, particularly in *Australuca, Thalassuca,* and *Amphiuca*, tend to raise the carapace on the stretched legs, slightly to considerably, either with each wave or during a series of waves. While all of them give a low, chiefly vertical wave, the cheliped is sometimes swung obliquely outward to a semi-lateral position during its elevation; this occurs when the object of the display, whether potential threat or potential mate, is passing to the side or rear. None of these shows any trace of a circular lateral motion of the cheliped, nor do special display movements occur before copulation. Except in individual *bellator* (*Australuca*), copulation occurs at the surface, as described above.

In the remaining subgenera, the display is definitely lateral and, in its extreme form, includes high circular motions. Circularity is present in at least some part of the display in all American crabs, except in *Boboruca*, in which the jerking display unfolds the cheliped obliquely upward, somewhat as in an exaggerated Indo-Pacific vertical wave, and returns it in the same plane to rest position. In addition, lateral-circular waves occur in *triangularis* and *lactea* in the Indo-Pacific, these two forms belonging to the subgenus *Celuca*, which is otherwise American.

One point of particular interest is the occasional occurrence of the vertical type of wave, characteristic of socially less advanced forms in the Indo-Pacific, in the displays of highly specialized species which at moderately high intensities make lateral waves. Every lateral-waving species known to me by more than the briefest observation proves to have these subsidiary displays, always exceedingly similar to those of Indo-Pacific vertical wavers. Always they occur either during low intensity display, or among juveniles, or in both these situations. Often the atypical vertical display is combined with feeding. When moderate to high intensity phases of either threat or courtship take place, the wave form changes promptly to the lateral motions more characteristic of the species.

In contrast, lateral displays never occur among the most typical vertical-wavers, either in young crabs or during periods of low intensity. On the contrary, whenever weakly lateral tendencies occur, they are elicited at rather high intensity only, when a potential opponent or possible mate is passing to the side or rear; it is always a poorly developed, oblique, lateral-straight wave, tending toward component 4, and never a lateral-circular-wave.

A prevalent variation with lateral-waving species is the frequent change with intensity from lateral-straight waves to lateral-circulars. Sometimes the circularity is so slight that it becomes apparent only in detailed film analysis. This is especially true of some of the jerking *Minuca*. In *speciosa* (subgenus *Celuca*), Salmon (1967) noted the tendency for the wave to return to rest position in the same plane in a threat situation (here called a lateral-straight-wave), and to be circular in courtship.

In lateral-wavers, the female is attracted close to the burrow of the male. After intensification and often specialization of his display, he descends. Sometimes she follows him below, where in completed courtships copulation occurs. The preliminary specializations of visual display include special steps, stamps, or kicks of the ambulatories, rhythmic lowering of the carapace in curtsies, and vibrations of the cheliped, which are often visually conspicuous as well as acoustically efficient.

Herding (visual display component no. 14) is a variety of courtship behavior which appears to occur only sporadically in the genus, and is known among both vertical- and lateral-wavers. When it does occur successfully, it must replace the precopulatory behavior characteristic of the species. It apparently occurs only in certain populations, or at least is more frequent in some than in others. First observed in *stenodactylus* of the subgenus *Celuca* (Crane, 1941.1), it is now known also in *Minuca*, represented by Florida populations of *burgersi*, *rapax*, and *pugnax* as described by Salmon (1967), as well as in seven additional species, as shown in Table 20 (Crane, unpublished). Completion of the pattern, where the male succeeded in bringing about the descent of the female ahead of him into his burrow, has so far been observed only in *stenodactylus* and in *bellator*; in the latter species the entire puzzling sequence was filmed.

The timing of display, as suggested above, is so variable that it is disappointing as a refined taxonomic character, while its evolutionary aspects remain obscure. Few general statements can be made, in spite of the modest but well-distributed amount of sampling that has been done. It is true that the fastest waves are non-jerking verticals not raised far off the ground. Lateral waves are, in general, slower than verticals, but in highly evolved species the tempo is sometimes rapid, as in *beebei*, where most waves are completed in less than a half-second. Slowest of all are the multiple jerks of *rapax*, which at most, for an entire wave, clock at about 6 seconds, and at slowest at the rate of only one complete wave every 18 seconds.

Waving in general, particularly in socially advanced species, is speeded up not only by higher temperatures but especially by the heightened intensity of advanced courtship. Pre-combat threat waving sometimes approaches but never exceeds the speed of display in the last moments before a male descends his burrow, after he has attracted the near approach of a female.

Under natural conditions waving occurs only by day. A correspondence between its time components and the rate of sound production occurs in *tangeri*, as already noted on p. 480.

When motion picture films are analyzed, the variations in timing even of parts of waves are striking. This remains true when the films have been made of waves of approximately the same intensity, in similar social situations, and photographed at similar temperatures. When different intensities are compared, even greater ranges expectably occur. The parts of waves, such as upstrokes, temporal divisions by jerks, duration of pauses at peak of wave, and duration of the downstrokes also vary extensively, as do pauses between waves. When populations are compared that are well separated geographically, the range of temporal characteristics is likely to be further extended.

In some species wave counts and timings show a wider range in the systematic treatment than under the corresponding listing in Table 19. This discrepancy is due to the fact that the description of waving display includes both field notes and the results of film analyses, while the table is based only on film analyses.

In order to obtain adequate statistical material, unrealistic amounts of film would need to be exposed with the most exacting attention to factors of ecology, breeding season, distance of population from limit of range, semi-lunar rhythms, tidal conditions, sunlight, temperature, time of day, and social situation. Subsequent analysis of a caliber to uncover all but the grossest differences would have to employ the usual, time-consuming, single-frame techniques. It is difficult to see how the most generous and intelligent use of computer time could curtail the necessary preliminaries sufficiently to make feasible a study of adequate scale to give reliable data for comparative ethology. In short, my current conclusion is that time samplings, as presented in the recent papers of Salmon and his co-workers, by von Hagen, and in the present contribution should be continued at present—and only temporarily—on a very small scale, and that it be considered of minor importance even as a taxonomic tool, particularly in the study of allopatric populations. This course should provide extra time needed more immediately for basic experimental work. When this research has disclosed the essential factors in the timing of displays, it will then certainly be feasible to collect and process adequate data for rewarding results.

This program would parallel the course which seems currently needed in considering display color in *Uca* (p. 468). Contrary to earlier expectations, color has turned out to be of little use in taxonomy and a variable attribute of questionable importance in social behavior. As in display timing, both the physiological investigations and the experimental work on behavior remain to be done.

During earlier work on fiddler crabs, I was convinced that waving display not only is species-specific, but that the characteristics most distinctive to the human observer hold throughout the species range. This conclusion undoubtedly holds true for many species, including several with an extensive geographical range. One such form is *tangeri*, found from

Spain to Angola. In split-frame motion pictures, showing waving individuals from Portugal and Angola side by side, waves of similar intensity match each other almost precisely. This stretch of coastline covers some 46 degrees of latitude. Here, with the possible exception of extremely rare accidentals, *tangeri* is the only *Uca.*

On the other side of the Atlantic, *rapax* provides a contrasting example. This species ranges from north-central Florida to southern Brazil, a distance approaching the latitudinal distribution of *tangeri.* Throughout the tropical part of its range, some local populations of *rapax* mingle with those of *burgersi,* although the latter species is found characteristically in biotopes that are slightly more sheltered and less saline. The favored biotopes of both species do show wide zones of merging, although as usual in such cases the species for which the habitat is the more suitable predominates. In other examples, contiguous populations of the two species are often in full sight of each other, without visual obstructions. Similar situations occur more rarely in overlapping or contiguous populations of *rapax* and *mordax.*

Throughout this western Atlantic range, the number of jerks in *rapax* is extremely high, while the jerks in both *burgersi* and *mordax* number only up to four or five, during both unflexing and flexing. In comparison, *rapax* shows at least six jerks while unflexing, and the more usual number approaches 20. (Crane, unpublished; see p. 193.)

In eastern Florida, one limit of the range of *r. rapax*, distribution coincides for a short distance with that of *p. pugnax*, which is its allopatric representative in the temperate zone (Tashian, 1958). Here *pugnax* shows little or no trace of jerks, while in the north its jerks are definite (Tashian, 1958; Crane, 1943.3). These examples show how local differences in wave characteristics help to differentiate the visual displays of otherwise similar sympatric species. They give excellent illustrations of the principle of emphasized distinctions in zones of coincidence.

The question of display intensity in *Uca* is both important and difficult. Differences result in many display variables, of both timing and components, all of which often shift gradually into one another (Fig. 88 *A*, *B*). In spite of efforts, it has proved altogether impracticable to set up, for the species descriptions, criteria of "typical intensity." Yet, as any observer will agree, the species of *Uca* on a given stretch of shore can all be readily distinguished as far as they can be seen, providing only that the individuals are waving at moderately high intensity.

There is no doubt but that eventually species descriptions will precisely and reliably present the essential features of waving display. That time, however, will not come until electrophysiological work unites with experimental ethology in determining the important releasers among sympatric species. At present we know from experiment that the sight of the major cheliped under certain conditions releases aggressive behavior in males which are in the requisite physiological phase. We also know that any crab within a size-range appropriate to the species, without a large cheliped and passing or approaching a male in suitable condition, sometimes elicits courtship behavior (Altevogt, 1957; Salmon & Stout, 1962; Crane, unpublished). Beyond these beginnings the field is clear.

In conclusion, waving display should undoubtedly be regarded as species-specific, providing only that typological definitions are avoided and three circumstances kept in mind. First, the observed samples of display in a given population must include high intensity courtships. Second, the waving displays of a number of populations must be compared through as wide a geographical range as possible, just as in the case of morphological characteristics. Third, the displays of the other species of *Uca*, living within sight of a given population, must be taken into account; this caution is, of course, even more important in the case of closely sympatric forms.

G. CONSTRUCTION ACTIVITIES BESIDE BURROWS

I. *Introduction*

A few species of *Uca*, along with many other littoral and terrestrial crustaceans, sometimes pile up some kind of structure close to their burrows. Examples are known, for instance, in gecarcinids (Silas & Sankarankutty, 1960), while the well-formed "castles" of certain Indo-Pacific and West African *Ocypode* sometimes make striking additions to a sandy shore. Linsenmair (1967) found that in *Ocypode* the structures played an important role in reproductive behavior, having signal functions both between males and in courtship.

In *Uca* the structures take the form of walls completely surrounding the mouth of the burrow, here termed a *chimney*, of a rough little *pillar* beside the burrow, or, in a further development of the pillar, of a symmetrical and smoothly arched *hood*; the latter is always concave on the side closest to the burrow.

These structures have three features in common. With two known exceptions, they are erected only by adults, whether females or males, and at least in the males only by individuals in breeding condition. Second, construction of chimneys is sporadic throughout the genus. Third, pillars and hoods, although almost entirely confined to certain species of the subgenus *Celuca*, are absent over whole areas of the ranges of the species, apparently without regard to ecological differences. They are also absent in part of a population or within populations in a majority of displaying individuals. Fourth, all of the structures, except for some material in chimneys in at least *arcuata*, *forcipata*, and *urvillei*, are made by carrying substrate with the ambulatories of the minor side from beyond the burrow to its edge, not from below ground.

II. *Chimneys*

In the subgenus *Deltuca* chimneys are characteristic of at least breeding females in *arcuata*, *forcipata*, and *urvillei*, and in some populations of *coarctata*; all these species are allopatric forms. The only examples known of constructions by young *Uca* are found among them: In Hong Kong I saw two very small *arcuata* females building chimneys. Similarly, in Fiji only a few young *c. coarctata* of both sexes built chimneys; no structures were found around large burrows. The subspecies *coarctata flammula*, in northwest Australia, apparently makes none at all. Chimneys are also sometimes built by (*Amphiuca*) *chlorophthalmus*. In America the structures seem to be confined to the Pacific-Atlantic subspecies, (*Boboruca*) *thayeri umbratila* and *t. thayeri*, and to (*Minuca v. vocator*). The building behavior of *vocator ecuadoriensis* in the Pacific, if any exists, is not known.

III. *Pillars and Hoods* (Pls. 48 *B*, 49)

These two categories represent varying degrees of quality in the same type of structure. They are fashioned only by certain displaying males in the subgenus *Celuca* and, in *Minuca*, only in *minax* and, from one observation, *pugnax* (p. 202).

The distribution of the structures in *lactea* is of particular interest. Many displaying males of *l. lactea* were making large, well-formed hoods in northwest Taiwan in May and of *l. annulipes* in West Pakistan in June, although not in September. In north-central New Guinea several structures, more like pillars than hoods and not as high as their builders, were discovered during June and July in a population of *l. perplexa*; this particular group of fiddlers was subjected to prolonged, daily observation during the period and it would have been impossible for me to miss any additional construction activity. In spite of careful search from Fiji to Zanzibar, wherever displaying populations of *lactea* were encountered, no other examples have been found.

In the tropical Atlantic the structures occur in *leptodactyla* and *cumulanta*, and in the eastern Pacific, in *beebei*, *latimanus*, and *musica terpsichores*, always in the usual scattered distribution.

H. PRECOPULATORY BEHAVIOR AND COPULATION

Under this heading are listed, first, the species on which observations have been made. There follows a consideration of behavioral components that are included in display—whether visual, acoustic, or both—in which the male appears to be directing them toward a particular female, and which may therefore be termed courtship components. Mating sites are then discussed along with the associated behavior of courted females. The section closes with a description of the assumption of the position for copulation—apparently the same throughout the genus.

High intensity courtship behavior has now been observed in 25 of the 62 species recognized in this contribution. Copulation itself was first described by Pearse (1914.1), who observed *pugilator* in the laboratory. Pairings on the surface of the ground that showed every evidence of being complete are now known from field observations on 20 species as follows: in the subgenus *Deltuca*: all eight species (present study); *Australuca*: *bellator* (present study); *Thalassuca*: *vocans* (Altevogt, 1955.1, 1955.2, 1957.1; present study); *Amphiuca*: *chlorophthalmus* (present study); *Boboruca*: *thayeri* (present study); *Afruca*: *tangeri* (Altevogt, 1959; von Hagen, 1961, 1962; present study); *Uca*: *stylifera* (Crane, 1941); *maracoani* (Crane, 1958; present study); *Celuca*: *pugilator* (Burkenroad, 1947; Salmon, 1965); *beebei* (Crane, 1941); *stenodactylus* (Crane, 1941); *lactea* (Altevogt, 1955; Feest, 1969); *Minuca*: *vocator* (von Hagen, 1970.3). For a general account of mating in the Brachyura, see Hartnoll, 1969.

Caution is always needed in attributing to normal courtship any display component or other activity. In the displaying portion of a thriving population the individuals are constantly reacting toward neighbors and nearby wanderers of both sexes. Under these conditions both conflict and displacement behavior are sometimes prevalent. Consequently difficulties arise in interpretation, particularly but not exclusively when the species or subspecies is poorly known and observation time is limited.

Special caution is also needed under crowded conditions when it is not known whether or not the male in that particular taxon sometimes or usually courts with the dorsal part of his carapace directed toward the female. When he does so, the carapace is tilted more or less vertically, exhibiting a conspicuously large area. I have seen this posterior orientation used by males at least rarely in one or more species of every subgenus, and its use may be a general component characteristic of the genus; its prevailing use seems to lie in first attracting the attention of a passing female, especially when the male is already engaged in a threat display toward another male in front of him. In such cases the male sometimes then swings around and proceeds with characteristic frontal courtship behavior. In other examples the rear view is presented to a passing male. In a few species, however, notably (*Thalassuca*) *vocans* and (*Celuca*) *beebei* the male vigorously displays so often with the female behind him that it must be considered a regular part of the species-specific courtship pattern. In these exceptional cases display toward the rear has been observed in the field when no other individuals of either sex were nearby except for the courted female—a situation giving, of course, the most reliable evidence of a component used in courtship. I have also seen it in the New York crabberies when (*Minuca*) *minax* displayed in this fashion a number of times when no other crabs shared the tank with the single pair under observation.

Most display components as mentioned earlier are ambivalent (p. 495; Fig. 95). In the great majority of species a burrow-holding male increases the tempo of his display whether he is threatening another male or directing his activities toward a particular female. Not only does he wave faster, but his display motions are usually accentuated, the cheliped reaches higher into the air, and the wave when of a lateral type becomes more spacious, the form of the change depending on the shape of the wave at low intensities. The change often proceeds from a straight lateral motion, as in *speciosa*, in which the claw returns to the flexed position through the same arc at which it was extended, to become at high intensity definitely circular. If the wave is already somewhat circular, with the tip of the chela sketching ovals in the air, the narrow diameters become broader while pauses between waves are shortened; in (*Uca*) *maracoani* and its allies the ovals at high intensity become almost fully circular and continuous, with the chela tip directed almost straight upward (Fig. 88 *C*). Some specific characteristics of low-intensity waves are accented, either through prolongation of a pause at the wave's apex or increased speed in a vibratory component. Sometimes, as in *lactea*, the wave is elided altogether, being replaced by other motions. In a number of *Celuca* major-manus-drumming or its ritualized counterpart, then not acoustically functional, also increases in prevalence. All of these signs of high-intensity display are changed little or not at all when unequivocal courtship is under way.

In contrast, only several components of waving display appear to be restricted to courtship. The only widespread example is the curtsy, as it occurs in (*Afruca*) *tangeri* and in several *Celuca*. In *Minuca* this component is also present in the repertory of several species, but in each it is ambivalent. Another courtship component of waving display is the quivering of the outstretched first ambulatories in *oerstedi*; their anterior surfaces, along with contiguous parts of the carapace and buccal regions, are bright blue to human eyes and particularly conspicuous. A third courtship component is the vibration of the stiffened ambulatories on the major side in *saltitanta*, just before a male precedes an attracted female down his burrow; whether or not the motion produces sound is unknown. Finally, a special development of display toward the rear seems, at least in *beebei*, to be characteristic of courtship alone; in this species the male revolves in front of the female; only from the rear is the vivid green on the carapace visible, along with the purple aspects of the legs. Unfortunately, this juxtaposition of color and motion remains only a challenge for future work; experiments on the possible role of color in the social behavior of *Uca* have not yet been undertaken.

The well-substantiated cases where sound plays a definite part in the final stages of courtship are confined to (*Afruca*) *tangeri*, (*Minuca*) *pugnax*, (*Celuca*) *pugilator*, (*C.*) *speciosa*, and (*C.*) *cumulanta*. In these examples sound tapes have been secured during well-established instances of courtship. The work with *tangeri* was reported by Altevogt (1962) and von Hagen (1962), with *rapax*, *pugilator*, and *speciosa* by Salmon & Stout (1962) and by Salmon (1965, 1967), and with *cumulanta* in the present contribution. The results in *tangeri* and *pugilator* are discussed by Salmon & Atsaides (1968.2), as well as in the systematic section of the present contribution under each of the species concerned. Altevogt, von Hagen, and Salmon and his co-workers consider that the sounds they recorded were wholly or partly concerned with courtship, particularly at night. The examples of sound production with which I am familiar, whether recorded or inferred through stridulatory or drumming behavior of the individuals, were for the most part made during agonistic or, at most, ambivalent situations. The matter is further discussed under sound production (p. 481); see also under *tangeri* in the systematic division (p. 121).

The methods of proven sound production that are certainly used at times in courtship consist of major-manus-drumming in *tangeri*, *pugilator*, and *cumulanta*, and of leg-wagging in *pugnax*. Proved use of sound in the final stages of courtship is to be expected in many other species, but to date the evidence is observational only; sound tapes secured from activities of other species were made either during potentially ambivalent situations on the surface or when the crabs were underground, with no evidence available as to the particular stimulus situation, if any, that elicited the sound. It should also be pointed out, as stated under the descriptions of display behavior in a number of species of *Celuca*, that a number of my early descriptions of drumming ("rapping") with the major cheliped in courtship situations were based on faulty observation. When the films were analyzed, the motions were found to consist wholly or partly of ritualized drumming, with the cheliped not coming in contact with the ground. In other cases mero-suborbital contacts, not drumming on the ground, were products of the observed vibrations (pp. 226, 244, 245, 483).

In three of the nine subgenera copulation appears always to take place on the surface near the female's burrow. These groups, all confined to the Indo-Pacific, consist of *Deltuca*, *Thalassuca*, and *Amphiuca*. In the fourth Indo-Pacific subgenus, *Australuca*, copulation seems characteristically to occur at the surface, but several times a male was seen to edge a female more or less forcibly toward his burrow and push her down ahead of him.

In the remaining subgenera—*Boboruca*, *Afruca*, *Uca*, *Minuca*, and *Celuca*—circumstantial evidence indicates that the crabs habitually copulate underground in the burrow of the male, after the female has been attracted by waving display and, sometimes, by sound production. Copulations that appear complete occur rarely at the surface in each of these groups. (Notably, in [*Minuca*] *vocator* von Hagen [1970.3] found surface copulations to be prevalent in certain populations that inhabited areas where dense vegetation restricted vision.) The majority of copulatory positions attained, however, are imperfectly oriented or the assumption of position is incomplete; in particular the abdominal flaps of one or both partners fail to be extended away from the sternum. These pairings appear to break off prematurely, and most often represent attempts at copulation by aggressive wanderers (see below). Incomplete surface copulations apparently occur less rarely in the subgenera *Afruca* and *Uca* than in *Minuca* and *Celuca*.

Nocturnal copulation at the surface appears to be usual in eastern United States populations of *pugilator* and *pugnax* and in Spanish populations of *tangeri* (Burkenroad, 1947; Salmon & Stout, 1962; Salmon, 1965, 1967; Salmon & Atsaides, 1968.2; von Hagen, 1961, 1962); in these species nocturnal sound production is prevalent, replacing waving.

One continuing need in the study of *Uca*'s courtship behavior and copulation is the use of infrared instruments during observations at night. There is no question, thanks to the contributions just cited, but that nocturnal courtship does occur in at least temperate populations of the listed species. These authors have all also reported actual copulation at the surface. Males of all these species, however, during the day attract females underground, matings at the surface being certainly rare, except in von Hagen's report of Spanish *tangeri* (see present contribution, p. 120). It seems possible that at least some of the reported pairings above ground at night are incomplete copulations performed by wandering males, or with females not wholly receptive, as occurs also at the surface during daylight. Use of adequate infrared illumination, now available but apparently not yet used by observers of *Uca*, should settle the relative numbers of complete and incomplete copulations in darkness.

The point is, of course, of particular interest in relation to the apparent advantages of underground mating; with temperate species the short breeding season may be offset by the addition of nocturnal reproductive activity (see Salmon, 1965, and present contribution, p. 176). If so, it is difficult to understand why sound could not wholly replace waving, attracting females underground instead of only to the vicinity of the males' burrows; undoubtedly sound in some species of *Minuca* and *Celuca*, both temperate and tropical, almost or wholly replaces waving in daytime in the final moments before the male descends and the female follows. The final selective step, it seems, could well have been taken long ago, with mating underground following acoustic components of courtship.

The behavioral role played by females in courtship remains largely unknown. The most prevalent and conspicuous form of female courtship behavior is the wandering stage of receptive individuals. This activity does not seem to exist in Indo-Pacific subgenera, in which the male characteristically does not attract the female to his own burrow but instead approaches and mates with her on the surface. In *Afruca*, *Uca*, and, especially, *Minuca* and *Celuca*, on the other hand, the great majority of courtship activity is directed toward wandering females (Pl. 50). The situation in *Boboruca* varies and needs further observation. In exact contrast to wandering males it is the wandering females that are always, and, in some species at least, uniquely responsive to the male's courtship display and that eventually sometimes follow him into his burrow underground. In species where the pattern is best known and, perhaps, best developed an experienced human observer can detect a receptive female at a distance without binoculars, not merely by the increased intensity of the display of the males among which she passes (p. 495) but by her own movements. Her progress is characteristically in short spurts, often somewhat jerky, with her body held low on the ground and her ambulatories little extended. This is the opposite of her non-receptive posture where the legs are spread stiffly and the body raised high; it will also be noted that this attitude is closely similar to that of a male in submissive posture, as when a non-aggressive wanderer passes close to a waving burrow-holder (Fig. 84 *C*).

A wandering female often progresses for many yards through displaying populations, sometimes not pausing at all, but eventually stopping to feed and perhaps take over an empty burrow far from where she was first observed. Usually her course zigzags, as she dodges among groups of males excited by her passing. Sometimes she is briefly attracted by an individual male, as shown by her pausing and perhaps approaching closer to his burrow. Less often she approaches closely enough to elicit any high-intensity courtship component in his repertory before he descends his own burrow; usually the female then moves on; rarely she follows him below. If she does so she usually remains only a few seconds; this stay is presumably not enough for successful copulation, judging by the longer periods observed at the surface. Very rarely the male plugs up the burrow after the female has descended and neither crab emerges during the remainder of that period of low tide.

In the subgenera confined to the Indo-Pacific the females are far less active and wandering seems to be minimal or absent. Sometimes individual pairs maintain adjacent burrows for several days or more; in a population of *chlorophthalmus* in New Guinea the record for a single pair was four weeks—from one new moon to the next. In that population, as well as in others of the same species, of *dussumieri*, and of *coarctata*, courtships were observed repeatedly between members of the same pairs of neighboring residents. This behavior occurred on two or three successive days during favorable semi-lunar periods.

In all the subgenera a male is often stimulated to intensive display by a nearby female that suddenly emerges from a burrow and moves, even when normally feeding, either briefly toward a male or past him. Under these conditions the male's burst of activity is usually short.

We still know almost nothing of the requirements for receptive behavior in the female. Feest (1969) published a study on the ontogeny and sexual biology of *triangularis* and *lactea annulipes* in southern India. Information on the physiology of reproduction is not included, but clear data are presented showing peaks of copulation and egg-bearing around new and full moon. In *triangularis* maxima occur in July and October, during each of the monsoons; *l. annulipes*, she found, breeds throughout the year. Data are given on numbers of surface copulations observed in the field between March and May in *l. annulipes*, in relation to the moon, hour, tides, and weather, but, as the author states, the table serves to indicate days on which strongly increased sexual activity was observed in the males. The question of completeness of these surface copulations and a description of any special activity of the females are not included in the discussion. Both early and recent contributions on other species, principally those of the temperate zone, only indicate that breeding seasons reach peaks in the earlier parts of the northern summer; no precise work has yet been carried out (p. 441). All observers agree that in *Uca* females mate when the carapaces are hard; this is in contrast to some other brachyurans (Hartnoll, 1969 and refs.).

Ryan (1966) recorded for the first, and apparently only, time the occurrence of a pheromone in decapods, a swimming crab in Hawaii. He concludes "these experiments indicate that a pheromone in the form of a sex attractant permits males to detect the premolt condition of *P. sanguinolentus* females. This does not eliminate an important role of submissiveness or other behavior on the part of the female in mating. These experiments also indicate that the pheromone is released through the excretory pores. Origin of the pheromone, its chemical nature, and the way it is detected by males remain to be determined."

On the basis of my observations both in the Trinidad crabberies and in the field it seems likely that a similar mechanism may operate throughout the genus *Uca*. Two facts are suggestive. First, in the crabberies individual adult females of *maracoani*, *chlorophthalmus*, and *dussumieri*, after spending several days underground, emerged from marked burrows slightly larger than before but with hard carapaces. It was these individuals that caused intense courtship activity by conspecific males which were also well established in the crabberies and individually known through carapace markings. The second suggestive fact is that in both *vocans* in Fiji and *lactea* in New Guinea, males sometimes herded females (p. 496); when I captured these females, all proved to be slightly immature; the examples examined totaled about seven in each species. In New Guinea I kept additional, herded, immature *lactea* in our small field crabberies for more than a week (until our departure terminated the work) in the hope that these individuals would molt; although they did not do so, this circumstance is without value because of inadequate conditions in the crabbery.

Judging by the examples seen of copulation at the surface, the position assumed appears identical throughout the genus. Once the two sexes have come into contact, the subsequent pattern consists of two stages. First, the male climbs the carapace of the female from the rear. The female, when receptive, remains in a more or less normal rest position with her carapace horizontal; her legs are bent and held close to the body, which almost or quite touches the ground. The male advances until his front is at least at the level of her mesogastric region. With his minor cheliped he usually taps or strokes the anterior part of her carapace and often plucks at it. In females having pile in the area at least some of the motions are directed toward this pubescence; when pile has been abraded, or when it is not characteristic of the species, the male often makes precisely similar motions; observations have been insufficient to determine the patterns more definitely; it is nevertheless certain that whether or not pile is present and plucked at, or whether the female's carapace is clean or muddy, the male often carries his minor cheliped toward his buccal region, making feeding gestures that are sometimes complete and sometimes show the incompleteness often found in ritualized patterns. The male's ambulatories, either singly or in various combinations, meanwhile almost always make stroking or tapping motions. (Fig. 89 *B*, *C*.)

In the three eastern Pacific species—*stylifera*, *beebei*, and *stenodactylus*—in which I have seen copulation at the surface, the female's ambulatories also rubbed against those of the male. I have not observed these species during copulation since originally describing it (1941.1), and it seems likely that the female's motions in each case were actually part of her non-receptive pattern; perhaps they included agonistic stridulation (p. 484) against the ambulatories of the male.

After some seconds or minutes of stroking, plucking, or tapping with the minor chela, the male turns the now quiescent female upside down and holds her at an angle to the ground while the abdominal flaps of both individuals project from the sterna. In all the examples I have seen the male both turns and holds the female with his ambulatories alone, the major cheliped being held flexed, in rest position. Altevogt (1955.1, 1955.2), in contrast reported that male *vocans* used the major cheliped to seize the female and hold her in place; later both Altevogt (1959) and von Hagen (1962) saw the claw similarly used in *tangeri* while Darwin (1871) speculated that some such use would be found for the major cheliped. It seems likely that the instances observed by Altevogt and von Hagen were examples of the unusual behavior that crops up so frequently among aggressive wanderers (pp. 507, 687).

Only the tips of the gonopods are inserted in the gonopore and, in the species where the thumbs are reduced and arise far down the shaft, it seems that these elements cannot be functional; it is worth noting that variation is usually characteristic of thumbs in these positions.

In surface matings the crabs remain in contact for periods ranging up to an hour or more (von Hagen, 1962 and present study). Sometimes, for whatever reason, the copulating position is held for only a minute or so. Pairs in which the gonopods are apparently fully engaged can sometimes with care be approached and picked up.

The form that copulation takes underground is unknown, since the necessary arrangements for observation in crabberies have not been performed.

I have seen ovigerous females copulating, particularly in *vocans*, and spermatophores are often found in place in preserved ovigerous specimens throughout the genus.

I. RHYTHMS OF SOCIAL BEHAVIOR

The effects of temperature, tides, rainfall, and light on activity in *Uca* were discussed in an earlier chapter (p. 440). Here their social aspects will be reviewed. Social activity throughout the genus is largely confined during the daytime to several hours before and after low tide. As the water begins to ebb, almost the only activity of all members of the population is feeding, with, sometimes, minor excavations of the burrows from which they emerged. Although some individuals continue waving display until the water almost touches them, most again feed and deepen the burrows during the last hour or two of rising tide. Some species attain the peak of their waving activity at least an hour before low water; others are most active shortly after the tide has started in.

Social activity at night never includes waving display, but at least some species substitute acoustic components during nocturnal courtship (refs. on p. 504). The hours before midnight are, so far as known, those during which most acoustic activity takes place.

Acoustic responses from within the burrow to an intruder have been elicited experimentally by day as well as by night in a variety of species (p. 481).

Intermale combat of all kinds seems to peak during the day, about an hour earlier than waving display for the species; in any case it virtually vanishes within an hour after low tide. Neither combat nor threat behavior has been directly reported at night, although von Hagen (1962) reports the emergence of male *tangeri* at night in response to surface drumming by another male.

Recent laboratory work on endogenous circadian activity rhythms (Barnwell, 1968.2, and refs.) shows that a maximum is apt to come in the morning and a second, minor peak around sunset, with minimal activity in the early hours of the afternoon. This result agrees with my field observations (Crane, 1958, and later, unpublished); these indicate that when low tide occurs between about 1300 and 1600 social behavior is less than on other days, even when all other factors, such as temperature, are favorable.

It also agrees with observations of Altevogt, of von Hagen, and of Salmon and his associates on the beginning of nocturnal acoustical activity at dusk, although this can also be interpreted as a response to decreased light. Experimentally these investigators have induced the diurnal substitution of sounds for waving merely by covering a visually displaying male with a box (Salmon & Atsaides, 1968.2, and refs.).

A few field and crabbery observations show in addition that a pre-sundown period of increased waving sometimes occurs when the tide is low at that time. Both Altevogt (1957.1) and I have noted it in *vocans*, in India and Fiji, respectively. Pre-sundown waving is particularly evident in at least Trinidad populations of *thayeri*, where I have checked it sufficiently often to be certain of its regular occurrence. I have also noted it sporadically in a number of other species, in several subgenera. *U. thayeri* is one of the forms in which the peak of waving activity occurs, when the tide is favorable, as early as 0700 to 0800.

In general, the period of maximum social activity takes place fortnightly when low tide falls during the full daylight hours between about 0800 and 1200. On many shores, where the tides are those characteristic of many, rather even, continental coastlines, this period begins a day or two after new and full moons. Because of the simultaneous occurrence of both a response to the ebbing tide and to change of light, it now seems feasible to eliminate the idea of a third, semi-lunar factor to explain the high degree of social activity when low tide falls in the morning; mutual reinforcement of circadian and tidal endogenous rhythms appears a sufficient explanation.

It is worth noting that representatives of more than 20 species maintained a fortnightly rhythm when they were kept for weeks on an unnatural tidal schedule. The phenomenon was observed in crabberies out-of-doors in Trinidad. Although the water level was lowered only once a day, during the morning, and raised in the afternoon, the peak of waving and other social activities still occurred on days close to full and new moon. The conditions and observations were not sufficiently continuous and complete to warrant formal presentation here. The effect, however, was so reliable that it was used to schedule in advance concentrated periods for observation of waving by individuals flown to Trinidad, over a period of five years, from overseas. The crabs came from the eastern Pacific, Japan, and the Philippines, all, by chance, from shores where spring tides, following new and full moons, occurred in the morning. All the fiddlers accommodated within a few days, as usual, to both the local light cycle and to the single low-water period provided every morning. For weeks, and, in a few cases for almost a year, they continued to show clear traces of the fortnightly rhythm in their waving display, courtship behavior, and construction of towers or pillars on the edges of the holes. This effect corresponded to that already reported (Crane, 1958) in the same Trinidad crabberies when *maracoani* and other local species were provided with normal tidal cycles.

Investigation of rhythms in populations from shores with single, diurnal tides and from those with minimal tidal effects are now beginning to be made (Barnwell, 1968.2 and refs.).

In the tropics social behavior, including reproduction, continues all the year around, unless it is locally impeded by monsoon floods, as in southeast Asia, or by drought, as for *Minuca* in some parts of the neotropics. Here, when conditions are favorable, the crabs emerge and feed, but they often do not wave at all for weeks at a time, while combat and other forms of social behavior are minimal or absent. In the subtropics such as in the southern half of Florida, social behavior is strongly reduced or absent only during the winter. In at least some subtropical populations, combat and occasional waving appear seasonally before courtship, as was shown in *inversa* when a population was observed in Mozambique in late August, at the species' southern limit (Crane, unpublished).

In temperate populations the actual breeding season is apparently restricted to one or two months, although waving and incomplete courtships extend throughout warm weather. Adequate data are still not available even for the northeastern United States. During the summer of 1968 I observed the onset and development of social behavior in *pugilator*, on the northern boundary of its range. Waving appeared in some individuals at or soon after on their first appearance following hibernation, at the end of May; yet throughout the breeding season, ending in early August, combat behavior was almost lacking, except for a small amount of burrow seizing from small crabs by larger individuals; the minimal, ritualized combat between males peaked in mid-June, as did the infrequent waving displays and high intensity courtships. Non-social activities, however, including feeding, burrowing, and quickness of response to moving objects appeared altogether normal.

J. PHASES OF SOCIAL BEHAVIOR

In addition to the rhythms described above, all tropical fiddler crabs sufficiently studied prove to have individual, endogenous phases which pass from below-ground inactivity through one or more days of unusually long periods of feeding and passive sitting to a wandering phase. This is succeeded by at least two social phases, that of aggressive wandering and that of waving display and mating in association with a particular burrow. Each has been already characterized in detail in preceding sections on combat, waving displays, and copulation. An intermediate phase, marking the onset of territoriality but without waving, is present or absent. When present, it may be demonstrated only during part of a single period of low tide. These elements are known in moderate detail only for *maracoani* (Crane, 1958 and Figs. 92, 93), but all of the elements have been exhibited, both in the field and in crabberies, by examples of all the subgenera. The phases are recurrent, and of such brief duration, at least in the tropics, that they cannot be due simply to the seasonal state of the gonads. It may well be that in the temperate zone, where the breeding season is short, no such differentiation exists. The point obviously needs study.

Under crabbery conditions, dominance hierarchies are held at most for a few days. Crabs at the top of the day's hierarchy are almost always in full display phase, in which the crab waves and defends a territory. Only when in this phase does a male copulate, although males in the phase of aggressive wandering often try unsuccessfully to do so. The burrow held by a waving crab is then often the center of combat between the two; occasionally the wanderer seizes the burrow, but if so, he soon abandons it. Males at the peak of a display phase sometimes continue to wave vigorously at times of the day when other members of their species are inactive.

Crabs in the non-social phases are unaggressive, move about with the body held close to the ground, and sometimes remain secluded for days in their burrows. These periods underground are only rarely associated with molting.

Accumulating examples indicate that capturing and handling active crabs, whether they are aggressive wanderers or displaying individuals, sometimes alters their subsequent behavior, changing their phase to one less active socially.

Droving, rare in the genus as a whole, shows intermediate characteristics. The participants are obviously in a phase at once non-aggressive, non-territorial, and non-waving; yet the movements, somewhat synchronized as they are, are unmistakably a form of social behavior.

A final phase variation needing comment has been only briefly observed in the Indo-Pacific. Rare individuals, showing every other sign of being aggressive wanderers, wave as they walk even when nowhere near a burrow they have occupied. Altevogt first reported such behavior in *vocans* in India (1955.1, 1955.2). I have also seen it in *vocans* in Zanzibar, as well as in *dussumieri* in the Philippines and in *urvillei* in Zanzibar. The two subgenera concerned are *Thalassuca* and *Deltuca.*

K. UNUSUAL BEHAVIOR

The term *unusual behavior* may perhaps serve less inaptly than some other heading for this section, covering the range of examples better than *abnormal activities*, for instance, or *irregular patterns.* Still, the choice is really a catchall to cover our ignorance. Once we understand the circumstances under which an activity occurs, even if the function remains obscure, the bit of pattern usually fits into the ethological scheme. Also, once we have learned something about it, we may meet it often, as with a new word mastered and adopted with enthusiasm.

A good example is the "posing" of fiddler crabs. Observers now and then come upon a *Uca* that spends many minutes without moving and is unusually slow to take flight. The individuals most likely to attract attention are large males as they stand beside their burrows, bodies raised, major chelipeds extended up and out, and their carapaces tilted toward the sun. Almost any population visited several times will yield at least one conspicuous example. A number of writers (Pearse, 1912.2, 1914.2; Crane, 1943.3; Altevogt, 1957.1; von Hagen, 1962) commented on the habit. Pearse's suggestions that it might be a threat posture or part of courtship proved unsatisfactory and the behavior remained unexplained. Jansen (1970) has now found that posing, at least in temperate zone populations of *U. tangeri*, occurs before the molt, and summarizes his findings in part as follows (p. 58):

> The concentration of the hemolymph is correlated with external factors (salinity, temperature) and the moulting processes. Changes of environmental salinity lead to adaptive hemolymph concentration by ional shifts, but there is no shift of the hemolymph water content. . . . There is an adaptation to the seasonal temperatures in *Uca tangeri* leading to a rise of upper thermal death limits during the summer. *Uca tangeri* regulates its body temperature by transpiration, extrusion of buccal foam, and sheltering in places of favourable microclimate. Posing is due to a deficiency of water- and ion-balance. It is only during the premoult stages that a critical hemolymph concentration is met with in *Uca tangeri*, and only during this time the crab is especially sensitive to environmental concentration.

The seasonal changes described cannot be responsible for the prevalence of posing also in the tropics, but Jansen's work certainly provides the key to the behavior as it occurs throughout the genus. Posing can no longer properly be listed as "unusual behavior," although before Jansen's explanation I probably would have included it among the examples below.

Most forms of behavior that both occur infrequently and remain unexplained are probably activities of males in the aggressive wandering phase (p. 687). A striking example is given by Pearse (1912.2), in his account of fiddler crab behavior in Manila:

> Some of the activities of the fiddlers were like those displayed by higher animals while at play. The crabs frequently darted about apparently

> without a serious purpose, and were sometimes downright mischievous. On one occasion a male was half-heartedly pursuing a female. She went to her burrow, secured a plug near by, and shut herself in. The male then came directly to the burrow, seized the plug, and cast it to one side. The female was just emerging from the burrow when the writer ended the episode by frightening the participants by a sudden movement. Another time, two males (an *Uca marionis nitida* and *U. forcipata*) of medium size were seen running about for perhaps half an hour over an area about 12 meters in diameter. They kept close together and acted like two mischievous sailors ashore. The tide was coming in rapidly, and in their rambles the pair came to a place where a large slow-moving *U. forcipata* was carrying a plug to close his burrow. They waited until the plug had been pulled down over the owner, then the *U. forcipata* went to the hole and removed it; and, as the outraged owner emerged, the plug remover and his mate scuttled off toward the former's burrow some 4.5 meters away. He soon closed his own burrow, for the advancing water threatened to inundate it, and his companion hurried away down the *estero*. The writer watched him until he had gone more than 11 meters and was lost to view at the edge of the advancing water. To all appearances activities such as these just described were carried out in a spirit of sport.

The account is more revealing than Pearse's later (1914.2) shortened version of the same episode, since the quoted paragraph gives the distances traversed by the fiddlers. This progress through the population, the "half-hearted" pursuit of the female, and the generally destructive character of the males' activities are frequent characteristics of aggressive wanderers. I have never seen two such males moving about close together as Pearse described, but any one who spends enough time watching fiddlers will not be greatly surprised by the account. Such an observer may also sometimes decide not to delete the anthropomorphic comparisons that turn up in his field notes; much of the lively variety of activities in a group of fiddlers is peculiarly difficult to convey in undefiled scientific terms.

A second example I would also now unhesitatingly attribute to the crab's being in an aggressive wandering phase. The episode took place in Panama and the male fiddler concerned, *U. musica terpsichores*, was individually known to me from observations made on several previous days on the same spot. In this account (Crane, 1941.1: 160), the word *shelter* was used for structures beside the burrow now termed *pillars* and *hoods* (present study, p. 500).

> One of the most individualistic, inexplicable performances I saw was that of a moderate-sized but apparently adult male *terpsichores*. His display coloration was not well developed on the day in question, his usually white carapace being heavily streaked with dull yellow and his cheliped scarcely pink. He did not build a hood or display, but enlarged his burrow and fed energetically. Then, suddenly, he went straight over to the newly erected shelter of a neighbor fully eighteen inches away. Without any provocation or preliminaries he undermined the shelter from the rear and pushed it down on top of its owner; the two crabs then spent 15 minutes fighting, in the course of which both darkened rapidly, losing all trace of display coloration, and the shelter owner lost the tip of his pollex. Finally, the aggressor let the owner go, then went directly to the next hood, six inches from the first, and repeated the episode exactly. In this case, too, the owner was powerless and was constantly thrust down his own hole, although he put up a good fight. At last, after another 25 minutes of uninterrupted struggle, the aggressor released this crab also, and returned, without any hesitation, to his first victim, who by now was cleaning himself up and had regained most of his display coloration. At the approach of his former antagonist, the victim tried to flee down his hole, but was seized from behind. Another duel, lasting no more than several minutes this time, followed, and ended as on the first two occasions by the aggressor's abruptly releasing his victim. This time the former returned slowly but directly to his own hole, cleaned himself, and began to feed. Neither of the two victims rebuilt their shelters on that day, although the tide was only slightly past dead low at the time.

On another visit to Panama in 1957 I observed similar behavior in a male *beebei*, which pulled down and stamped on the pillar of a neighbor; as in the male *m. terpsichores* described above, the *beebei* neither displayed nor built a pillar on the day concerned.

As suggested in the section on precopulatory behavior, it seems likely that the seizure of females in the large cheliped observed by Altevogt (1957.1) and von Hagen (1962) may also have been performed by aggressive wanderers.

In an early paper (Verrill, 1873) appears an account of fiddlers' taking bits of vegetation down their burrows, presumably for use as food. I have not been able to check this behavior in *Uca*, although it has also been reported in several popular accounts and I have seen examples of it in *Ocypode gaudichaudii* in the eastern Pacific. In Tahiti a small land crab (Gecarcinidae) appeared by daylight at the mouth of his burrow as soon as I dropped a red pen beside it; this he seized in his claw and dragged underground.

As a final example the following observation made in Fiji in 1965 (unpublished) will end this section, which could continue at great length. It concerns courtship behavior that became irregular, in *c. coarctata.* A male and female, with burrows about 18 inches apart, performed a sequence I have not seen in any other *Uca.* For about ten minutes they had been in copulatory position beside the female's burrow, the normal location in this species. Possibly disturbed by me, the female suddenly went underground and the male returned to his own burrow and also descended. Five minutes later the female emerged, went straight to the male's hole, and reached down it with the ambulatories of one side. She then returned to her own burrow, moving fast. Meanwhile the male surfaced promptly, followed her as he waved, caught up with her close to her burrow's mouth, and they started mating again.

L. SUMMARY

The categories of social behavior distinguished in *Uca* consist of droving, agonistic postures and motions, sound production, combat components, waving display, construction activities, and precopulatory behavior. Several of these classes include many different components; 14 agonistic postures and motions have been distinguished, 13 components of ritualized combat, and 14 of waving display exclusive of timing elements. In addition, 16 methods of sound production are enumerated, counting both those known through tape recordings and those presumed to occur from combined morphological and behavioral evidence. When to all these figures are added the several components in each of the remaining categories, the number of known components in *Uca*'s social repertory totals more than 70; at least 50 of them certainly occur in each of a number of species. Many of the components are widely distributed throughout the genus; some are ubiquitous; a few are apparently restricted to several species. Almost all social patterns are connected at least indirectly with reproduction. The majority are concerned with aggressive behavior rather than with courtship; others are ambivalent, including most components of waving display. Only a few are confined to courtship. Social behavior is controlled by a number of rhythms, all more or less endogenous. They include responses to tidal, circadian and seasonal factors; in addition there is possibly a separate semi-lunar rhythm. At least in the males of many tropical species, individual rhythms are responsible for short behavioral phases, mating behavior being restricted to a period termed the display phase. Many examples of unusual behavior are probably due to a male's being in the midst of an aggressive wandering phase.

Chapter 6. Territoriality, Functions of Combat and Display, and the Origins of Social Patterns

OUTLINE

A. INTRODUCTION

The last chapter examined aspects of social behavior which could be objectively described. In colloquial brief, it dealt with the *whats* and *whens* of these patterns. This chapter, in contrast, deals with the *what fors* and the *how comes*, which, together, constitute the *whys*. Both subjects obviously demand speculation, which in many contributions can be quarantined at the end. In this discussion such a course would be illogical and confusing, since the heart of the subject consists of speculation. Therefore I have tried simply to base most non-factual statements directly on objective knowledge which is either reviewed in the same section or else supported by references given to other pages; more general speculation is, I hope, labeled with clarity.

The chapter, then, will attempt to make some sort of functional and evolutionary sense from the wealth of variety in the social life of fiddler crabs. Looked at as a whole, this variety is astonishing. The components reviewed in the preceding pages listed seven general categories—droves, threat postures and associated movements, sound components, combat, waving display, constructions beside burrows, and copulation. Fourteen different threat postures and motions emerged; 16 methods of sound production were counted, both proved and assumed; 15 components of combat were described, along with 18 components of waving display.

In combat alone, 84 different morphological specializations were designated on the claws; sometimes more than 40 of these structures appear in a single species. Some of the combat components should in time certainly be subdivided, as they become better known, and the 84 structures on propodus and dactyl could even now, by viewing them differently, be increased with propriety, without further knowledge of their functions.

At the end of the chapter a review of the rhythms influencing the timing of social behavior added more complexities to the subject. Occurrence of the various activities is controlled by endogenous rhythms responsive at the least to tidal levels and to light. In addition, a separate factor of temporary, recurrent, physiological phases is individual and apparently wholly under internal control. We have also noted that social behavior is not always closely connected with the state of an individual's gonads, although practically all of it is confined to populations in their breeding season.

Because of its association with all forms of social behavior in *Uca*, territoriality becomes the subject of the first section of the present chapter. The second division discusses the functions, known and suspected, of the social patterns, while the final section considers the role of ritualization and other factors in their evolution.

B. TERRITORIALITY

Although one useful definition describes a territory as "any defended area," the phrase is somewhat inadequate for use in discussing fiddler crabs. A review of various aspects of territoriality in the genus must, in fact, make use of most current concepts of the subject, as well as of related topics.

One of these related aspects is covered by the term "home range." It applies very well to the basic condition of entire local populations of a species, where in any one low-tide period most individuals are neither waving nor fighting. Instead, they pass the greater part of their time in feeding close to the burrow in which they spent the preceding period of high tide, and at most wander, feeding, nearer the water's edge. This minor wandering depends both on the individual's phase and on the richness of the substrate in providing food close to the burrow. During an aggressive wandering phase, the range extension is among displaying males of the local population, usually higher on the shore, rather than down near the low-tide level. Thus the home range of an individual may change from day to day, and may usefully be viewed as almost the same as that of the local population. In these terms it normally extends throughout the local area that is ecologically suitable for the population. Where such a biotope is extensive, as on a long strip of homogeneous shore, it is possible that no single individual ever travels throughout the area, even during several wandering phases. The necessary work with marked crabs, started by Altevogt (1954), remains to be done. When it is, care must be taken either to avoid handling during marking, or to allow several days for the released crabs to recover before relying on any data collected. This procedure is essential because of the effects of handling on the crabs; the indications are strong that their individual phases are affected.

Animal territories in the more restricted sense may be divided into three general groups, each of which helps fulfill several related biological needs. First, a territory often supplies protection from environmental stress and from predators. Second, it frequently promotes successful reproduction in a variety of ways; it may serve as a center to attract and stimulate sexual partners and to deal with male intruders, threatened or actual; the resulting displays and combats almost certainly are mutually stimulating, regardless of their outcomes, and in many animals ensure fertilization of most females by the stronger or more energetic males; in some animals territories also serve importantly as centers for rearing the young. Third, a territory may aid in the distribution of individuals in a population in accordance with the food supply.

In the coming discussion, the view is presented that in *Uca* only the first two categories are chiefly concerned. All three will now be described as they occur in fiddler crabs.

1. *Basic Territoriality: The Burrow as a Shelter*

For these crabs as for numerous other intertidal animals, the burrow is primarily a protection. During high tide it provides shelter against aquatic predators, and during low water against the triple threat of desiccation, heat, and terrestrial enemies. Burrows serve these functions whether or not a crab defends a particular hole.

Most individuals during most low-tide periods remain unchallenged holders of the particular burrow from which they emerged when the water receded; they feed in the neighborhood, excavate the burrow a bit, and retire into it as the tide rises. A break in this pattern usually comes only if the resident enters a wandering phase, or if it is dispossessed.

A crab that for any reason lacks a burrow generally has little difficulty in finding a new one. Biotopes normally have more burrows than crabs when the tide is out, since some wanderers always move out of their holes as the water level falls. A burrow that gives even a fair fit will be taken over and remodeled as needed. A corollary is that although any crab except the smallest can, capably and in minutes, dig a new one, a burrowless crab, unless he is in an aggressive phase, with few exceptions hunts first for an empty hole. This habit has perhaps adaptive value through conservation of time and energy, when all activities must be accomplished during short periods.

Very young crabs do not use burrows at all. When pursued or when overtaken by the tide, they simply sink into the damp terrain wherever they happen to be. Herrnkind (1968.2) gives data on the instars at which laboratory-reared *pugilator* start to dig burrows.

When feeding far out on the moist flats, alarmed crabs sometimes sink into the substrate in a fashion used by the very young. When such a crab returns to the burrow area ahead of the rising tide, it does not necessarily approach its former burrow, but seeks out an empty hole, as described above. Sometimes, as repeatedly noted in a northern population of *pugilator*, the burrowless crab quickly ousts a smaller crab by prying it out with the major cheliped or digging it up with the ambulatories. In the examples observed, the dispossessed individual, always in a non-display phase, either sought an empty burrow nearby or, often, ousted a still smaller crab. In each case, there was no sign of protest by the evicted individual. The final, smallest crab in such a series several times sought shelter under a shell. In each example the dispossessions took place low on the beach, close to the level of the rising water. Females as well as males were dug up, but I never saw a female oust a male; sometimes they traveled many feet before finding an empty burrow of suitable size.

When startled or pursued in the burrow area but at a distance from his own hole, a fiddler often shelters temporarily in one already occupied. When an intruding *Uca* enters such a burrow, the resident makes acoustic signals. If the alarm persists, the signal stops and the two crabs temporarily tolerate the double occupancy. Usually the intruder emerges and moves away soon after the emergency has passed. When an intruder is suddenly and somewhat forcefully inserted by an investigator, sounds of scuffling often follow and normal acoustic signals are lacking.

This acoustic warning system is clearly genus-wide. Specific differences in the recorded signals have not yet been investigated, nor is it known how both signals and tolerance levels vary with respect to size, sex, and physiological phase.

Since this kind of burrow defense takes place only below ground, the territory is obviously confined solely to the burrow itself.

II. *Display Territoriality: The Burrow as the Center of a Defended Area*

When a male crab becomes ready for courtship and mating, the mouth of a particular burrow quite suddenly becomes for him the center of a small territory which he vigorously defends on the surface, primarily through visual signals of threat and of waving display. Sound production at the surface, as well as underground, sometimes also plays a part in this second territorial pattern. Intermale combats occur in any part of the territory, but are usually close to the burrow's mouth; only in encounters between neighbors do they occasionally take place on the borders. Finally, in the subgenera which are socially most advanced, receptive females are attracted to the defended area where, in the ultimate stages of courtship, they are induced to descend the burrow by intensive waving and other motions, sound production, herding, or a combination of these activities. When the burrow serves, following successful courtships, as a mating site, it offers obvious protection.

In these advanced forms, too, the burrow mouth itself perhaps acts as a signal to the female. Perhaps it shows conspicuously as a dark object in the paler terrain, and so may direct or even attract her after the displaying male has vanished into it.

Adult females, especially when carrying eggs, uncommonly also defend burrows on the surface by means of threat postures, stridulation, and, sometimes, the interlacing of ambulatories in apparently forceful combat with other females. Almost nothing precise is yet known of the nature of territorial behavior in this sex.

The size of the defended ground around the burrow mouth varies widely depending on the species, the size of the individual and the degree of crowding on the biotope. The display energy of the crab on a particular day is probably also a factor. Usually a fiddler defends a small circle with a radius equaling several of his own widths, with the crab measured in the maximum stance of full display. In species of *Deltuca*, where the male pursues the female and display is vertical, the territory seems to be smallest, scarcely more than standing room with the cheliped extended in lateral threat position. In species with advanced display requiring more space, as in *stenodactylus*, the defended area is relatively much larger; an excited individual races back and forth, its elongate cheliped thrust out and up, and the crab probably covering more than six times its maximum dimension in an ordinary beat. When females defend a burrow on the surface, they confine their activity to standing-room beside the mouth.

In flourishing populations, boundaries of displaying males often adjoin and the territories are smaller. Females and young, passing or feeding, are tolerated close to or even within territorial limits; members of other species are similarly accepted, providing that a male is not closely similar in size and shape to the burrow-holder. Often, however, some of these tolerated individuals are warned off by low intensity threat motions when the resident male is feeding.

During the onset of display territoriality, fiddler crabs tend to go to the upper levels of their intertidal habitat or to pick some slight eminence for their burrow. This behavior probably has the double effect of giving them more time daily for display and acts, in combination with upward stretches of cheliped and body, to make them more conspicuous. Finally, the drier substrate doubtless provides a better resonator for acoustic drumming (von Hagen, 1962).

In many populations the very largest individuals are found farther from the water, often in quite unsuitable localities. In these cases the tendency to go higher seems to be an example of hypertrophied behavior, analogous to the impractically large chelipeds found in senescent males. If the territory is long held the crabs may be definitely undernourished, although this result has not been proved. Unexplained deaths, perhaps due to senescence in some sense, occurred almost daily during a week I spent observing *tangeri* in Angola. All the dead crabs were among the largest males, all occupying a row of the highest burrows, along the upper edge of the intertidal area; each day a few of these large crabs were in the display phase, but no females were ever seen to approach the zone. All of the nine dead crabs examined had atrophied digestive glands (livers). A similar state was found in a number of large *maracoani* kept for months in the Trinidad crabberies; these individuals, also, occupied burrows on the highest available substrate, and occasionally displayed one day and died the next.

Another such instance of the hypertrophy of this part of territorial behavior was well shown by a single large *demani* male near Davao in the Philippines. He waved, almost without rest periods, all during the single low-tide period of observation. His burrow mouth surmounted a nearly desiccated elevation. No other member of his species was closer than 50 feet, and all were lower down on damp ground, suitable for feeding. Presumably the lone male's display area was covered by water at times of spring tides; at present however there was no trace even of other burrows.

The frequent concentration of displaying males in a restricted section of rather high ground superficially resembles a lek formation. It must be emphasized, however, that these gatherings have not yet been found to be characteristic of all observed populations in even a single species. Very often the displaying males are scattered, although in clear sight of one another, throughout the greater part of a population. The relative breeding success of individual males with burrows in different locations has not yet been investigated.

Females in breeding condition in some species, particularly in the socially less specialized subgenera of the Indo-Pacific where mating takes place on the surface, occupy burrows close to those of waving males. In the advanced groups, receptive females move actively through the displaying part of the population. After mating, while the eggs are developing, they usually inhabit burrows closer to the low-tide levels than those of any other section of the population.

Early reports (Schwartz & Safir, 1915 and ref.) state that single males and females occupy the same burrow for indefinite periods. The instances I have found of pairs in burrows are of three kinds. First, a female, after an apparently successful courtship, often or usually stays in the burrow with the male throughout the following high tide; this statement is based on about eight reliable field observations of five species in assorted subgenera, as well as on at least that many others in the Trinidad crabberies. Second, I once collected a series of about 50 adult *ornata* in Panama; three of the burrows were occupied by adult pairs; none held two crabs of the same sex; the three pairs had perhaps been startled by my approach or had just mated. Third, as described earlier, when fiddlers are startled while feeding away from their burrows, such as when a human being approaches, they take refuge in any nearby burrow of convenient size, regardless of the presence or sex of its occupant; I have often collected such individuals. It seems that future investigators of the duration of double occupancy by pairs should take special care to exclude startled crabs from the data.

A display territory may be defended for only part of one low tide, or held for many weeks. Often territory-holding, as in *Scopimera* and *Dotilla*, is so temporary that a new burrow is dug at every low tide. Then the crab sinks and twists in a characteristic fashion wherever it happens to be when nearly overtaken by the rising water. Burrows in these genera, as in *Uca*, are defended at the surface only by crabs in display phase.

Species of the *Uca* subgenera *Deltuca* and *Thalassuca* do not usually keep the same burrow more than a few days. Often in *vocans* and other species living close to low-tide levels, burrows seem to be changed freely, even between low and high tides of the same day, and display territories are sometimes held only for part of a single low-tide, as I found definitely to be true in a few individuals observed in Fiji, during 1965. Long before, Altevogt reported (1954) similar mobility in the same species in western India, and, unfamiliar at the time with many other species, concluded that the crabs should not properly be called territorial. It is now clear, however, that true territorial behavior does occur, even in *vocans*, and that the duration of defense should be left out of any definition of territorial behavior.

A contrasting example was afforded by two *dussumieri* from the Philippines, a male and female. These crabs were kept for months in a Trinidad crabbery, along with a large and changing population of other species. The female moved the mouth of her burrow from time to time, laid eggs, and eventually died. The male, which came into the display phase repeatedly and maintained threat and combat relations with neotropical males of comparable size, kept the mouth of his burrow within an area of about 6 inches square for more than 6 months. The slight shifts in the position of the mouth usually occurred only after a fresh layer of mud was added to the substrate. This crab also went through brief phases of wandering and aggressive wandering from time to time, but returned to the burrow daily.

Additional examples of territories definitely held for more than one week include the following observations, each on only one or two individuals: *stylifera* in Panama (Crane, 1941); *chlorophthalmus* in New Guinea; and *arcuata*, *chlorophthalmus*, *maracoani*, *thayeri*, *rapax*, and *festae*, all in the Trinidad crabberies.

Numerous other observations both in the field and in the crabberies indicate that display territories in *Uca* are usually held for several days at most, throughout the period of one display phase. As in related areas of fiddler study, only extensive field work with marked crabs will give an accurate picture of the situation.

III. *Territory and Dispersal: The Relation of Burrow Defense to Food Supply*

In many animals territoriality is instrumental in distributing members of the population in accordance with the food supply, a view amply demonstrated in many of Wynne-Edwards' examples (1962).

In *Uca* such a spacing-out function may be performed by basic territoriality, where the burrow serves as a shelter. As described above, occupancy of a burrow by more than one crab is discouraged by acoustic signals. It is not yet clear why this is so. In at least one related genus (*Potamocypoda*, Tweedie, 1954; Crane, unpublished), large burrows are at least sometimes altogether communal. In these groups the individuals are all smaller than are most fiddler crabs, and all live in very wet, muddy environments, so that food supplies are probably more abundant than in the habitats of many *Uca.* In the latter genus, the adaptive value of single occupancy very likely involves efficient distribution and undisturbed feeding over an adequate-sized patch of terrain.

It does not seem possible, however, that either basic or display territoriality in *Uca* can ensure the maintenance, through successive generations, of a stable population consonant with the food supply on a particular biotope. As in most crabs, the larvae are pelagic, and there seems to be no mechanism for ensuring that surviving young are cast up on the parental shore. In addition, the population of a given strip of ecologically suitable shore must be determined primarily by the food supply available to the youngest crabs, near the water's edge.

Very young crabs do not fight and hold no territories. As the tide approaches, partly grown males at most sometimes take over burrows low on the shore from smaller crabs, which make no apparent effort to stay in possession, but simply move on to an empty burrow, or oust some still smaller individual of either sex.

In contrast, mature crabs in full display phase and defending territories high up on the shore often do little feeding and, since both growing algae and tidal jetsam are less abundant, have less food than do those farther down. These individuals sometimes leave their burrows and descend to feed among the non-territorials. The center of the breeding individuals usually lies in the middle parts of a habitat. Here, among the displaying males, non-breeding as well as receptive females are tolerated along with young of assorted sizes. The very young move about a lot, and females may or may not do so, depending on their phase.

These most actively breeding parts of a population do not usually contain the largest males, which more often are found on the highest usable terrain, only briefly moistened by the tide. Gigantic males, apparently senescent and perhaps undernourished but displaying characteristically and defending their boundaries from similar neighbors, sometimes are the only occupants of this unfavorable zone.

In short, display territoriality in *Uca* apparently does not at all promote an optimum distribution of a population. Basic territoriality on the other hand, in discouraging occupation of a burrow by more than one individual, may aid in distributing individuals over the biotope. It seems that neither form of territoriality, however, can play any part in keeping the population stable.

C. FUNCTIONS OF COMBAT AND DISPLAY

I. *Introduction*

The preceding section described the display territory as a center of social behavior, including visual threat display, sound production, intermale combat, and waving display. In this section suggestions will be made concerning the functions of all these activities and their relations both to territoriality and to one another. The basic question of the role of agonistic behavior in relation to courtship and reproduction will also be examined.

The selection of a logical order of comment is difficult. Combats rarely take place unless preceded by threat postures or by waving, and usually by both. Yet, as will be shown later, threat postures appear to be derived from combat while some waving components just as clearly are based on threat. Sound components crop up throughout the categories. On the whole, combat can be viewed as the most basic of the activities concerned, even though it occurs more rarely than any of the patterns, and, in its wealth of modern complexities, is certainly the most specialized of all.

The functions of intermale combat and its ritualizations, therefore, will be considered in the first two sections. Parts of both are taken with little alteration from a previous contribution (Crane, 1967), since they still express my present viewpoint. Several results of subsequent field studies are also briefly considered in these and later sections, because they affect some of the conclusions in the published paper; a formal contribution is in preparation.

II. *Functions of Intermale Combat*

Possible explanations of fighting remain far from clear. It is unsurprising that each crab coming into territorial and display phases acquires a burrow in a spot appropriate for display and mating. But there appears to be no need to obtain such a burrow through combat. As described earlier, there is never a shortage of empty burrows during a period of low tide. Furthermore, few areas are so crowded that there does not seem to be ample space, empty and undefended, among displaying males where new burrows could be dug.

Yet an aggressive wanderer, unless his aggressiveness has been reduced by a fight with a burrow-holder, either pays no attention to these empty burrows, or pokes into them with cheliped or ambulatories briefly and superficially; then he moves on.

Although occasionally an aggressive wanderer stops slightly longer at a burrow occupied by a nondisplaying crab, any attempt to dig out such a crab is rare and little effort is expended. I have never knowingly seen a combat between a crab that is not in display phase and a wanderer, or between two wanderers.

In fiddler crabs no harems are maintained and single females seem never to be direct causes of intermale combat. Occasionally a male even abandons an advanced courtship attracted by a combat between two other males.

The immediate goal of an instigator does not in fact seem to be the taking over of a suitable burrow as a center for display or a direct competition for females. Rather, the apparent aim is a combat with a displaying male.

The combat itself is characteristically partly or fully ritualized; only in *lactea* are components known that are at once forceful and stereotyped (p. 494); in most cases the combat results in no detectable change in the subsequent behavior of either crab. One or the other withdraws his claw from contact with that of his opponent; the aggressive wanderer resumes his progress through the population, threatening and entering into new combats; the burrow-holder promptly resumes display, its intensity undiminished. In one such *rapax* combat in nine, however, a wanderer's aggressiveness was reduced; in one in 45, the burrow-holder was dispossessed and the wanderer took over. Less intensive observation of other advanced species have yielded corroborative observations: the wanderer's behavior is similar and only rarely is there a detectable result. In those instances where a wanderer actually takes over a burrow he sometimes assumes the display phase at once; more often, he does not wave, but shortly abandons the burrow and moves on, his aggressiveness maintained and his territorial drive still in abeyance.

With these figures in mind it seems likely that combat may sometimes either advance or retard the assumption of territorial and waving phases by the wanderer. Summation, as suggested on p. 494, may well play a part here that the field techniques in use could only suggest. Combat, then, may serve as a mechanism for ensuring that suitable burrows for display are not taken over by males in subbreeding condition; nevertheless, the availability of empty burrows, noted above, forms an obvious argument against this view.

The function of combat will now be examined from the point of view of the burrow-holder. If this displaying crab is not vigorous enough or sufficiently motivated to fend off an aggressive wanderer, he may be in an inadequate condition for breeding and should not, from the point of view of selection, be left in a position to attract receptive females. Yet many vigorous burrow-holders, in other species as in *rapax*, withdraw partly or wholly from an incipient combat, even in the frequent instances where the approaching wanderer is the smaller crab; then the burrow-holders resume waving and courting promptly and strongly when the wanderer has departed. The role of this withdrawal behavior in the pattern of combat remains puzzling.

After combat, however, one *rapax* in six delays waving, while one in 45 loses his burrow, with a consequent postponement of resumed display. These relative numbers agree well with impressions received in numerous more casual observations of combat in other species.

In examining the possible selective values of fighting and its ritualization, a distinction should be kept in mind between these two visible results—namely reduced aggressiveness and delayed waving. Since all burrow-holders are in the display phase and, as part of that phase, in a threatening and fighting mood toward both aggressive wanderers and trespassing neighbors, it seems that a post-combat reduction in aggressiveness by a wanderer normally would result only if he were not ready for territorial-display-mating behavior. In that case the "loss" of a combat would be a selective advantage. On the other hand, a reduction of display time for a burrow-holder through prolonged combat would be a disadvantage.

A reasonable suggestion, therefore, appears to be that the ultimate value of combat, regardless of the role of ritualization, lies in preventing suboptimal males from wasting the breeding time of the population by attracting receptive females. This explanation does not, however, account for all the facts. It takes no account of combats, largely or fully ritualized and resulting very rarely in waving delays, between vigorous burrow-holders. Again, the function of down-pushes remains unexplained. Here one burrow-holder, far from endeavoring to take over the burrow of his neighbor or at least to dig the occupant out and engage him in combat, simply thrusts him forcefully underground before returning to his own burrow and resuming display.

When viewed as a whole it seems that the function of combat may lie primarily in stimulating and synchronizing mating behavior. As in so many other groups of animals where such an effect is suspected, proof awaits work in endocrinology and neurophysiology.

Similarly in need of the attention of physiologists are two strong impressions that recur during field work on *Uca*. One is that combat may serve to release tension in the actively courting section of the population. The other impression, particularly compelling when one is watching ritualized mutual encounters, is that combat appears often to be in progress for its own sake. The attention of a third crab is sometimes drawn to a nearby combat; he may then either interrupt or engage one of the participants after the end of the first encounter. Even more suggestive are the sequences of high ritualization discussed below. It is noteworthy that recent experimental work indicates the existence of an "appetance for aggression" in two species of fish and in squirrel monkeys (Thompson, 1963, 1964; Azrin, Hutchinson, & McLaughlin, 1965; Rasa, 1971); the subject is reviewed by Eibl-Eibesfeldt (1970: 326).

III. *Questions of Adaptive Values in Combat Ritualization*

As shown in previous sections, a large majority of combats in *Uca rapax* show no detectable element of force and hence may be termed fully ritualized. More casual observations on other species indicate that ritualization is similarly prevalent throughout the genus. Finally, in one component prevalent in *lactea* combats, force itself appears to be ritualized. In searching for the selective advantages of ritualization, the immediate effects of individual combats have proved unilluminating. As is well known, even the most violent fights in *Uca* practically never result in physical damage; no injury at all was ever seen in *rapax*. The exceptions are healed puncture wounds on a manus that are apparently inflicted by an opponent's chela tips. As soon as one learns their appearance, the small pits or discolorations can be found on occasional males in almost any collection of preserved fiddlers. I now suspect that the great majority are not received in combats on the surface. Instead, they probably result from the engagement of two claws in a burrow shaft, when a male reaches down and tries to pull another fiddler out. At least in a northern population of *pugilator*, I often saw young crabs dispossess still smaller crabs in this way when the tide was approaching (p. 511). Particularly if the burrow occupant has recently molted, an intruding claw might easily pierce the soft integument. Possibly a deep puncture would leave visible traces after subsequent molts (Pl. 46).

It seems, therefore, that a protective function, which has been considered obvious in the ritualized encounters of many well-armed animals, is not now of importance in fiddler crabs.

Again, the data on *rapax* give no evidence that ritualized encounters are any more likely than the uncommon forceful fights either to promote or to prevent behavior changes in an opponent. This is true in general both of reductions in the aggressiveness of a wanderer and of delays in resumption of waving by a burrow-holder.

In *rapax* the only apparent advantage of ritualization seems, rather, to lie in the shortening of combats. The counts so far made indicate clearly that ritualized encounters are not only far more numerous than those including components of force but also that they are shorter, most lasting less than 10 seconds. In contrast, forceful fights continuing more than one minute are usual. This is true whether or not a forceful combat results in subsequent visible behavior changes for either crab. While this difference in duration appears to have no obvious importance for an aggressive wanderer, the shortening of combats through ritualization may well be a selective advantage through its effects on burrow-holders.

This suggestion is based on both the ecology and the mating behavior of *Uca*. Since they court only during low tide, and are usually further restricted by other requirements, both meteorological and physiological, their periods for courtship and mating are limited. Combat and courtship cannot proceed simultaneously and, in *Uca*, the combats of males seem to hold no attraction whatever for females. Therefore it seems clear that, by shortening combats, ritualization ensures that courtship opportunities are minimally reduced.

It may be that an important factor in waving display lies in its stimulating effect on other males or in the synchronizing of breeding activities. Here, too, a shortening of each combat would advantageously shorten the time during which one or two wavers did not contribute to the communal effect.

An unresolved objection to the suggested advantages of shortened combats has arisen in my recent work (unpublished) on two species of the subgenus *Celuca*, *pugilator* and *lactea*. In these forms almost all combats take place close to the hour of low tide, while most waving displays and most courtships occur later. In two thriving populations of *lactea*, in fact, the last combat of the day and the first courtship were often separated by more than an hour.

One characteristic of ritualized combat becomes increasingly apparent with continued observation. This consists in the leisurely, formalized, and wholly unforceful cooperation sometimes apparent between the two opponents. A highly ritualized encounter in *rapax* may run about as follows. An instigator, whether wanderer or neighbor, approaches a burrow-holder. A rub by one or both crabs, outer manus against outer manus, usually follows. Next, the instigator sometimes holds perfectly still while his opponent slowly eases his chela into the actor's slide position; the two crabs may then reverse the role, the shift being accomplished slowly, without fumbling, and with the apparent cooperation of the crabs. In a few moments they may progress to a similar alternation of heel-and-ridging or, in hetero-clawed encounters, to an alternation of heel-and-ridging with interlaces. In other examples a single opponent may be the actor throughout, the second crab holding himself quietly. When the actor breaks off, both crabs move apart and resume their pre-encounter activities.

Observation of these encounters gives a strong impression that they provide one or both crabs with satisfactions that are not concerned in direct goals, such as taking over a burrow or evicting a trespasser; the activity itself seems to serve as the goal. Current work on *lactea* (p. 494) suggests that forceful combats also provide their own rewards. We know nothing at all yet about the means of conferring satisfaction—whether through the performance of the motions, or through the reception of associated sensory stimuli.

If ritualization does indeed sometimes operate selectively through shortening combats and thus providing more time for courtship, then an obvious pressure would be toward even shorter ritualized encounters. Ultimately the action might be reduced to a token touch of mani or single rubs of ridges by briefly overlapping chelae.

This trend is not apparent. According to our present knowledge, the socially advanced species have the largest repertoire of combat actions and the most extensive structural specializations for high-intensity encounters. If ritualization shortens combats, then further elaboration could nullify the effect. Occasional prolonged encounters in *rapax*, fully ritualized and elaborately mutual, suggest that this process may prove to be a factor in the continuing evolution of the species.

IV. *Functions of Threat Postures, Threat Motions, and Sound Production*

When the functions of threat postures, motions, and sound production are considered in relation to the above conclusions on combat, an obvious question arises. If ritualized combat is such a short, efficient, and pleasant way of stimulating, synchronizing, or otherwise promoting reproduction, why does threat behavior persist in the genus? After all, these postures and motions seem most effectively to discourage the realization of many potential combats. The apparent answer has a number of parts, based on both direct and indirect evidence and, ultimately, on speculation.

First, basic forms of at least visual threat display are certainly far older than *Uca*'s components of ritualized combat, which necessarily evolved in association with the specialized major cheliped. Schöne (1968) describes and illustrates the occurrence of basic agonistic postures in a wide variety of brachyuran crabs, including some fully aquatic forms; its prevalence as a behavior pattern throughout much of the animal kingdom does not need comment. It seems that such a basic form of behavior would be unlikely wholly to be eliminated from the genetic constitution of a small group.

Second, basic threat postures are used by fiddlers, as by other crabs, not only in intermale situations but also as a pre-final defense against predators (p. 473). Since actual seizing of an active threat—whether bird, crab-eating raccoon, or human finger—may well result in the loss of a slow-growing appendage, even if the crab escapes, the use of a strongly deterrent threat display appears to be a strong advantage. This fact alone would encourage the retention of at least the basic postures of lateral and frontal threat.

Third, as described on p. 479, threat signals are freely used in *Uca* not only between aggressive wanderers and burrow-holders, or between two burrow-holders, but also, at low intensities, in gently warding off an encroaching female or a young crab when a male is feeding. Sometimes both young and females use threat signals in similar fashion, as do members of two species sharing the biotope. Threat signals are also the primary means used by unreceptive females in warding off males. The use of auditory signals by burrow-holders underground, apparently to ward off intruders, was described on p. 481. Antiphonal sound production by male *tangeri* was reported by Altevogt (1964.1).

Fourth, successful threat displays obviate all risk of time-consuming forceful combats. Such is not the case with ritualized encounters, which neither always replace prolonged fights, nor always prevent a forceful ending to a combat with early ritualized components (p. 488).

Fifth, most threat signals are less time-consuming even than most full ritualized combats (p. 493), making more time available for courtship.

The sixth and last function of threat to be considered is wholly speculative. In common with other conspicuous or audible elements of social behavior, threat postures, motions, and sounds may well be part of the pattern of general social stimulation—to the actor, to his potential antagonist, and even to his neighbors. It will be remembered (p. 492) that at least one threat action, the after-lunge, is made by a burrow-holder after a combat; it is always directed toward the receding figure of his former opponent. Comparable behavior is of course exceeding common in a variety of animals. I have seen it a number of times even in rhinoceros beetles, in a pattern described by Beebe (1946). Always the component followed an intermale combat in which one beetle was, as usual in the species, taken between the "horns" of his antagonist and flung, upside down, to the ground. The successful beetle usually then moved his own body rapidly up and down several times, by stretching and bending his legs, somewhat as in fiddler curtsy components; all the while the beetle's head faced his upset opponent. As far as I know, the physiological explanations for such patterns have not yet been provided, and the components perhaps should not be included under threat behavior. Even if a mere release of excess energy, not then needed for further combat, is involved, the effect of further, stereotyped motion is also perhaps self-stimulating to the animal.

In summary, then, the above position on the functions of threat display in *Uca*, including postures, associated motions, and sound components, may be stated as follows. The basic postures of threat display, appearing widely among brachyuran crabs, provide defenses against predators through reducing the risk of injurious or fatal contact. Some visual and acoustic threat signals are of social use in fiddlers of both sexes and different ages. In agonistic relations between adult males, threat signals have two advantages over fully ritualized combats: when effective, they altogether preclude a time-consuming forceful combat, and they are usually shorter even than brief, ritualized encounters. Finally, it also seems likely that threat behavior, in common with other forms of social display, provides both to the displaying crab and to conspecifics stimulation that somehow promotes reproduction.

V. *Functions of Waving Display*

In the categories of social behavior so far discussed—combat and threat displays—there has been no question of ambiguity. All the components are directly associated with agonistic behavior, not with courtship. In the next category, that of waving display, the functions of most of the components are clearly ambivalent, since they are employed both in wholly intermale situations and in pure courtship (Fig. 95). As described elsewhere (p. 501), a few components occur only in courtship; they are then confined to periods of high intensity. On the other hand courtship in many species has no components differing from those of waving display directed toward males. Waving itself can and does take place out of sight of other displaying, or even apparently attentive individuals, and rarely in the Indo-Pacific even occurs without a display territory. A low-intensity, vertical form of waving uncommonly is seen even in immature individuals (p. 497). The functions of waving display cannot, therefore, be resolved in any simple fashion. According to our present understanding, its probable uses are as follows.

First, waving is an advertising display almost always indicating the presence of an adult male close to breeding condition and displaying close to a particular burrow at the center of a small defended area. There he will threaten or enter into combat with intruding males in appropriate physiological condition and, through increased intensity and often elaboration of the waving pattern, follow or attract potential mates. Waving serves, then, most obviously as an identification mark. This mark, just as in birds and many other animals, is treated quite differently depending on the sex and physiological state of the viewing conspecific.

Second, it seems unarguable in this particular category that the display is stimulating to females and, in appropriate species, perhaps the distinction should be made that it is also directive. With few exceptions, waving immediately precedes normal attempts to copulate. Again, wandering females often clearly change course and approach a crab that suddenly begins intensive display (p. 503).

Whatever future work discloses about lek-like characteristics in groups of displaying males, it seems probable that they will share with many highly developed lek patterns the advantage of arousing a female gradually to mating readiness as she wanders through the display area. So far there is no evidence that females are attracted most to males that are larger, brighter, whiter, more vigorous in their displays or with burrows near the center of the group.

Third, waving display often or even principally can be viewed primarily as a particularly efficient component of threat behavior that is confined to intermale situations. As listed in the fourth function of threat display (p. 517), waving probably reduces the frequency of actual combats, which do not at all attract females; unlike strictly threat displays, however, waving displays in highly economical fashion serve simultaneously to repel males and attract females. Thus, not only is time saved for courtship through the avoidance of long combats, but even the waste of momentary threat motions is usually eliminated. A short period of observation of any healthy population in actively breeding condition will strongly advocate this view: the intensity of waving is often or usually clearly increased by a burrow-holder at the approach of another male, even when the potential intruder's major cheliped is in full view of the waving crab. (Thus there is no question in these examples that the burrow-holder is temporarily mistaking the male for a female, as sometimes happens, stimulating the burrow-holder briefly to increase his waving toward the tempo of intensive courtship.) Very often the approaching male, whether a wanderer, aggressive wanderer, or neighboring burrow-holder, passes promptly on or withdraws, without stimulating the displaying crab to change his ambivalent wave to monovalent threat.

Fourth, whether waving is also stimulating to males is more debatable, since, as in combat and threat, evidence is lacking. Suggesting the probability of stimulation are populations in which waving display of moderate intensity is the only social behavior apparent for several hours at a time. Especially in socially advanced species of *Minuca* and *Celuca*, waving over entire display areas appears frequently to be uninterrupted by the approach of other individuals of either sex, combat and threat behavior often being virtually confined to earlier hours before the onset of waving. An excellent example is *lactea* (p. 292). At these times waving display should perhaps be regarded as another example of hypertrophied behavior, analogous to the ascent of old males to sub-optimal levels of the shore, rather than as a mechanism for stimulation. The concentrated waving occurs when the tide is already on the way in and does not seem ever to be followed by bouts of agonistic or courting activity at atypically late periods during the same low tide; any stimulating effect would have to carry over until the next retreat of the water. This protracted effect may well occur, however, the results of waving perhaps being cumulative over a period. The several examples of synchronous waving (p. 300; Gordon, 1958) I have seen have all been in prosperous populations in which aggressive wanderers were at the time scarce or absent and in which neighboring males stayed close to their own burrows. While the synchrony may have an effect only on females in the display area, it seems more likely that the males themselves are stimulated.

Fifth, even if there would be no interbreeding among sympatric species in the absence of waving, interspecific differences in waving display must be an important time-saver in the intertidal hours available for courtship. Females with only the rarest exceptions are not attracted toward males of other species and then only briefly (Crane, 1941.1 and unpublished).

Sixth and finally, waving displays may serve directly as one barrier to interbreeding among intermingled allopatric forms. These last two suggested functions will be considered further in the next chapter.

In summary, waving is an advertising display, almost always centered on a territory, and characteristic of a male ready to court females and to behave aggressively toward certain other males. Such display appears to be unquestionably important in directing the attention of receptive females and in stimulating them to cooperate in copulation. It also serves as a form of threat display toward other males, reducing the frequency of time-consuming threat displays and combats while simultaneously serving as a courting signal. It also seems to be a reasonable speculation that waving display, as well as threat and combat behavior, is stimulating to other males in or near breeding condition. Again, the existence of interspecific differences in waving apparently aid the efficiency of simultaneous breeding seasons among sympatric forms by avoiding incompatible courtships. Finally, these differences may serve as an important barrier in maintaining distinctions between closely associated populations of allopatric forms.

VI. *Functions of Display Territories*

The need remains to return to the role of territory in social behavior, this time in relation to the functions considered above of combat, threat, and waving display. Display territories may act, it seems, rather as artifacts concerned with reproduction. As such they have much in common with hypertrophied claws and complex display motions. All are devices which help bring males and females into a state of readiness for mating, ensure that potential partners are physiologically in condition for copulation, and, finally, bring the members of a pair together.

To go a step further, territories may be viewed as the ritualization of an artifact, a burrow, which most of the time is purely a genus-wide defense against predators and desiccation. Only during certain physiological phases of an individual is it turned into a status symbol. At these times, as already remarked, a combat, not a burrow, seems to be of prior importance to the crab.

It was also suggested that in socially advanced subgenera, in which the female follows the male below ground, the burrow mouth itself may serve as a sign stimulus to the female, perhaps merely as a dark object seen from crab height. In the ultimate specialization in this connection, it seems possible that vertical structures erected beside the burrow by some displaying males (p. 499) may be explained as ritualized burrow mouths, serving as supernormal sign stimuli. This explanation would not, of course, preclude their simultaneous usefulness as acoustic amplifiers, as suggested by Salmon & Atsaides (1968.2).

VII. *Conclusion*

When the complex of social patterns is regarded as a whole, it is difficult to avoid the conclusion that the varied activities have a stimulating effect on the population. The attractions of these views persist, in spite of our regrettable dearth of physiological data. I think that no one has expressed this attitude as well as did Fraser Darling, in a short paper entitled "Social Behavior and Survival" (1952), which in part is based on his earlier contribution on avian sociality (1938). In commenting on the latter paper Darling states:

> It held the dual thesis of the reality of social stimulation to reproductive condition in such birds as are social or colonial at some state of, or throughout, the breeding cycle; and the existence of a threshold of numbers in some colonial species, which might be critical as to whether the birds bred or not.
>
> Naturally, the extent to which the social factor enters into the life of birds varies greatly. In some it appears to be sporadic, in others seasonal, and in others it constitutes the whole way of life. Whereas the benefits of sociality in the lower animals as studied by Allee (1931, 1938) and others appear to be physiological in origin, operation, and result, the basic element of *stimulation* in avian sociality seems to be psychological and psycho-physiological. . . .
>
> The aggressive quality of bird song has, I think, been overemphasized. Proclamation, yes; *apparently* aggressive, yes; no more combative than a military tournament of befrogged dragoons, but probably even more stimulating. So-called fighting, and singing, are in my opinion often a form of social stimulation and have indirect survival value as aids to development of reproductive condition. I should think the term "aggressive behavior" could be dropped for a great deal of true display.

It seems that the above remarks apply as well to fiddler crabs as to birds and mammals.

D. Ritualization and the Origins of the Components of Social Behavior

I. *Introduction*

Anatomists usually trace with ease the descent of even the most unusual anatomical structures. Nobody argues with the conclusion that the "fishing-rods" on the snouts of angler fish, in spite of their worm-like bait and luminous bulbs, evolved from the first spine of the dorsal fin, which migrated forward and burst into specialization. The line of descent of the major cheliped in fiddler crabs is far more obvious. Although bizarre and hypertrophied, it undoubtedly developed directly from a homologous appendage found in numerous other animals. Segments have been neither added nor lost and there is no question, in spite of altered shapes, of their identities. Even the allometric growth of this appendage, so exaggerated in *Uca*, occurs to some degree in many other crabs.

Unlike the derivation of morphological characteristics, the evolution of behavior patterns is often compound in nature, and, in the absence of fossils, conclusions can never be proved to the satisfaction of everyone. The simpler movements involved in basic activities, such as locomotion, can usually be satisfactorily traced far back in an animal's ancestry. As soon as social patterns are considered, however, complexities multiply. Particularly in reproduction the sequences often turn out clearly to be formed largely from pieces of feeding, cleaning, fighting, and other behavior patterns resulting in curious hodgepodges that somehow work.

In the course of evolution these parts of patterns have with changed functions become simplified, exaggerated, or both. Hence they are termed *ritualized* in the senses used by Huxley (1914), Lorenz (1941), Baerends (1950), Tinbergen (1952, 1953), Huxley *et al.* (1966), and Eibl-Eibesfeldt (1970). Often, too, associated morphological structures are enhanced by increased size, altered shape, or changed color. Through these modifications they are made more conspicuous in visual display or otherwise contribute toward the production of an unambiguous signal in communication. These changes from the original form may be startling. Nevertheless, when a number of related species, in various stages of display evolution, are available for observation, the behavior in question can frequently be satisfactorily traced. And the evidence is often formidable. On such evidence the bases of ritualization appear most frequently to lie in intention motions and displacement behavior. These in turn typically result from situations originally involving inadequate motivation, conflict, or frustration.

In classic examples of the derivation of displays from such activities, Lorenz (1941) showed the development of certain duck displays from preening and Baerends of stickleback courtship from combinations of escape, fighting, and nest-building motions (Baerends, 1950; Baerends & Baerends-van Roon, 1950). Similarly Tinbergen (1952) traced the courtship of herring gulls through ritualization of postures showing conflict between tendencies to fight and to submit. In gulls food-gathering motions are also incorporated into courtship display.

In *Uca* striking parallelisms are apparent with such developments in vertebrates. Without the concept of ritualization, in fact, both the motions of the large claw and the subtler movements of other appendages would be unintelligible from the point of view of evolutionary biology.

II. *Displacement Activities*

Displacement behavior is not in itself a regular part of any social category, although it is often closely associated with threat, combat, and waving display. Because it plays, according to the view held in this contribution, such an important role in the origins, through ritualization, of many social components in *Uca*, an account of its characteristics has been deferred to this section.

This kind of behavior was first reported in the genus by Gordon (1955), who described incomplete feeding motions in *vocans* in South Africa. Displacement activities also undoubtedly occur throughout most if not all of the genus. I have watched them often in all species with advanced visual display that are well known to me, as well as in the intermediate *vocans*. They are of questionable occurrence only in *Deltuca* in the Indo-Pacific, the subgenus in which visual display is least developed. I have observed good examples also in the related genus *Ilyoplax*, both in the field in Japan, the Philippines, and Java, and in the crabberies in Trinidad.

Displacement behavior in the sense used here is defined as the release of energy, accumulated through the frustration of one or more drives, by activity characteristic of another drive. For instance, a bird often meets a situation where its urge to fight is in conflict with its tendency to flee. Under these conditions, it may stand still and preen its feathers or even go to sleep.

Fiddler crabs, depending on species and circumstances, often combine feeding or cleaning motions with waving display. They also sometimes stridulate or drum when the occasion does not normally elicit this response. Often these actions are incomplete or ineffective. In a typical example, a crab's minor cheliped, in a travesty of feeding motions, pinches air near the ground and then raises the claw toward the buccal area, where the third maxillipeds are appropriately ajar; the claw then is lowered, sometimes without even touching the mouthparts. Sometimes this feeding motion is even more sketchy, consisting of a brief, vertical arc of motion, all in mid-air. Much rarer examples emerged from a recent review of old motion picture sequences. These showed that several instances of drummings by the major cheliped were incomplete; the appendage, though vibrated, barely failed to touch either the ground with the manus or the carapace with the merus.

Displacement activities are usually clearly distinct from intention motions which typically are rather easily recognized as low-intensity, preliminary versions of actions that may or may not follow. They are also usually, but not always, distinct from the simultaneous performance of two different categories of behavior, most commonly true feeding and waving. In these situations, one pattern or the other usually proceeds at least at moderate intensity, while the second, although complete and efficient, is at low intensity. In the unequivocal examples of waving-cum-feeding, there is no apparent stimulus to waving display, in the form of either a threatening or approaching male or an approaching or attentive female. The waving continues at a low level, but functional feeding proceeds, normal pellets being rhythmically discarded.

In recent years a useful distinction has often been made between displacement and redirected activities. Examples of the latter term's use concern the substitutions of an inappropriate object as the focus of aggressive or courtship behavior which is frustrated in its natural expression. In fiddler crabs the displacement or redirection is often, in single individuals and within a few seconds, so rapidly changed and so often only partly ritualized, that it seems best to keep terminology at a minimum.

Such, then, is the type of material on which, I believe, are based many of the social components which have evolved in *Uca*. Even when in a given species a displacement motion has most clearly been ritualized into a characteristic part of some kind of display, its additional use as an occasional displacement activity is sometimes very apparent. When unfamiliar species are observed, a useful clue to the history of a puzzling action may sometimes be gained from color accents. If, for example, the minor cheliped is strikingly whitened, its use during visual display may well indicate ritualized motions rather than continuing displacement activity.

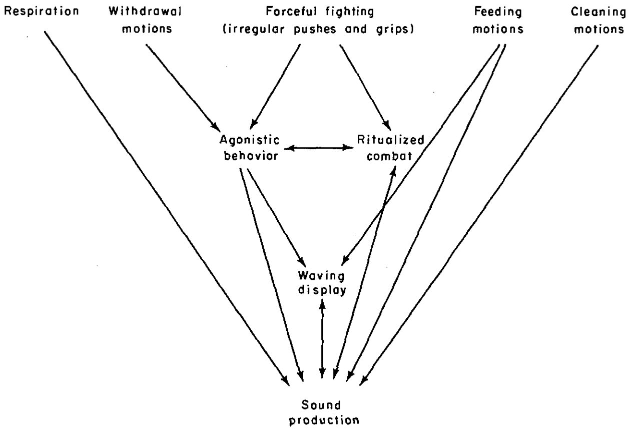
Sometimes an effective way of observing displacement behavior in the field is simply to watch or photograph the crabs at exceedingly close range. The procedure works reliably, it is probably needless to say, only with small, socially advanced species at the height of a vigorous display period. Their conflict, then, is between the urge to continue waving and the urge to retreat down their burrows. Under these conditions display sometimes becomes complicated by a variety of extra motions. When observation is based on a sufficient knowledge of normal behavior in the species and of other members of the genus, the atypical grouping of motions can be enlightening from an evolutionary point of view (p. 520).

III. *Derivations of Social Components*

The apparent origins of the components in three major categories of social behavior will now be considered. Combat, agonistic postures with their associated motions, and waving display will be reviewed in that order. Sound components both proved and, through morphological evidence, apparent will be apportioned among the several categories, since sound appears sometimes to have been the basis and sometimes a result of the development of a component belonging to another category.

Precopulatory and copulatory behavior are not included in the discussion because nothing is known of their form in underground matings. Furthermore, since we know nothing as yet of the part played by chemical factors in behavior, their possible role in the derivation of components will obviously have to be omitted. Once an adequate foundation of further research has been laid, future workers will doubtless find open to them another attractive source of reasoned speculation.

Suggested Derivations of the Principal Components of Social Behavior in UCA



For ease of reference all the components are relisted together in Table 21, numbered in accordance with their descriptions in the chapter starting on page 476. The table also gives page numbers covering descriptions in each category along with a reference to the earlier table showing their known occurrence in the genus. No table was supplied for the category erected for agonistic postures and motions because most of them are found widely or ubiquitously in the genus. When the posture is rare the known examples are mentioned in the discussion. For further ease of reference, each component name will be followed by its number prefixed by a letter: C for combat component numbers, T for threat, W for waving, and S for sound. The accompanying diagram shows the general pattern of apparent derivations.

(*a*) COMBAT

In the descriptions the first two ritualized components, manus-rubs and pollex-rubs (C1, C2), are regarded as low-intensity combat in distinction to the remaining high-intensity components.

It seems likely that the low- and high-intensity ritualized components have been derived from different sources. These are, respectively, from low-intensity, forceful manus-pushes and from high-intensity, forceful fighting with linked chelipeds. If, as seems certain, the usual direction in combat evolution has been toward the reduction of forceful fighting through ritualization, one logical point for the application of a deterrent would be immediately prior to the actual grip. The high-intensity components (C3-C13) all appear to have originated directly from unritualized forceful grips. All take place with the two claws partly or wholly in a position for grasping each other; when, rarely, a ritualized encounter proceeds to a grip, little or no change in basic claw position is made. As in social sequences in many other animals, the specializations appear to have been added one in front of another, the interlace (C9) being perhaps the closest now known to the original fighting grip.

Threat gestures in many animals are themselves certainly to be understood as ritualizations of fighting, where a weapon, impressive in size or other potential advantage, is effectively exhibited. By this criterion the threat gestures of crabs including *Uca* all qualify as ritualized fighting.

We therefore emerge with the following view. From forceful fighting in ancestral *Uca* were derived two apparently distinct classes of ritualization. The first consists of threat components, most of which, as will be suggested below, are derived largely from intention motions of fighting, including exhibition of the potential weapon. The origins of the second class, composed of the components of ritualized combat described above, are less clear. Ritualized they certainly are, in the sense that the original motions have been changed and the associated structures transformed. Yet no component of ritualized combat appears to be built on a pattern of frustration or on a conflict of drives, on intention motions, or on displacement behavior. Rather, it seems most likely that the principal roots lay in states of low motivation, the components evolving through the minute, cumulative advantages of brief, less-than-violent encounters, with actual contacts nevertheless at the usual points and along the usual edges. In short, when the doubtless more venerable threat components were not quite strong enough to control contact fighting, the forceful grips themselves became transformed into additional effective shorteners of the fray. But there is no likelihood that the two classes form a single sequence of evolution.

In the low-intensity combats formed by manus-pushes and manus-rubs (C1) a similar course of origin may be postulated. Here, again, the forceful push is considered basic; I have observed it, although casually and imperfectly, in several other ocypodids. In *Uca* combat its usual ritualized form appears to be the manus-rub (C1).

Three sound components, namely claw-rubs, claw-taps, and interdigitated leg-wags (S14-S16), are all associated with combat. The leg-wag is characteristic of females. Doubtless all developed in the closest association with the diminishing of force during the ritualization of combat. More specifically, it seems likely that the occasional occurrence of tubercles on areas of frequent contact during combat, and the consequent production of adventitious sound, led through natural selection to the variety of structures and behavior patterns now characteristic of ritualized combat. Since we know nothing yet of the role, if any, played by tactile stimulation, or indeed by sound production, in combat, further comment would be gratuitous.

(*b*) AGONISTIC POSTURES, ASSOCIATED MOTIONS, AND THEIR SOUND COMPONENTS

The first ten postures and motions (A1-A10) all have in common the prominent exhibition of the major cheliped and are hence confined to males. The first five of these appear to have as their bases rather simple motions of intention to fight with linked chelipeds, or to push away by force a potential opponent approaching, or being approached, from the front. The raised-carpus (A1) sometimes precedes high-intensity combat but more often leads to more intense frontal threat behavior (A2-A5), or to the forceful manus-push or to the ritualized manus-rub (C1); usually it subsides without sequel. In short, it serves as a non-explicit threat signal of very low intensity, with roots that are perhaps similarly plural.

The derivation of the down-point (A-2) if viewed from the point of view of *Uca* alone, appears to be much more directly concerned with high-intensity combat than does the raised-carpus, since it apparently always precedes high-intensity linkage of chelipeds in the four species where it has been observed. Thus it seems most likely that the component is derived rather simply from a motion of fighting; the linkage, when it takes place, proceeds directly from the posture, the four claw-tips coming into interdigitated contact as they leave the ground. An interesting point is that this posture, rare in *Uca*, is widely distributed in other Brachyura (Wright, 1968). Since actual combat is little or not at all known in these other examples, it is premature to comment further. The known examples in *Uca* are *maracoani* and *ornata* (subgenus *Uca*), *tangeri* (*Afruca*), and *inaequalis* (*Celuca*).

The frontal-arc (A3), with its to-and-fro warding-off motion, appears in contrast to the down-point (A2) to be derived from manus-pushing, rather than from high-intensity fights.

The forward-point and lunge (A4, A5), on the other hand, appear again to be intention motions of fighting. The after-lunge (A6) differs little or not at all from the lunge in posture and motion, yet its occurrence almost always follows an actual combat and is directed toward a retiring opponent. Once more, our ignorance of some of the factors makes additional discussion without value.

The carpus-out, flat-claw, and chela-out (A7-A9) each represents a progressive degree of withdrawal into the burrow by a burrow-holder when a potential opponent is nearby. Each of these components may be viewed most simply as a signal of readiness, of minimal intention, to fight; in form each is virtually only one of the preceding front threat postures, standing on end and reduced to minimum intensity. Sometimes only the extreme tip of the chela projects above ground. Consisting as it does solely of this motionless display of part of the potential weapon, each can also be considered an ultimate expression of a ritualized fight.

The lateral-stretch (A10), on the other hand, nearly ubiquitous in brachyurans, differs little or not at all in the social behavior of *Uca* from the threat posture sometimes assumed in the face of a predator. Here the threat is of injury to another species, but its origin in an intention posture of attack and display of the weapon appears similar.

Motions corresponding to the creep (A11) are so widespread in the animal kingdom that its occurrence in fiddlers scarcely needs further comment. It forms one more instance of the signal value of apparent size-reduction and withdrawal of weapon-display in situations requiring or inviting withdrawal from or appeasement of another's aggressive behavior. As in the high-rise (A13), below, its origins must lie in the practical importance for many animals of large physical size.

Although a true creep does not seem to occur in females, a low posture in this sex, as in so many other groups of animals, is a signal of receptivity.

The prance (A12), now noted with moderate care only in males of *maracoani*, *ornata*, and *pugilator*, will almost certainly prove to be of wide occurrence in *Uca.* At least occasionally it almost certainly is associated with the leg-stamp (S11), which sometimes, in the absence of any apparent surface stimulus, appears to be directed toward an individual underground. The same posture used in threat situations between males within sight of one another sometimes show the turned-under dactyls not quite touching the ground, and therefore incapable of producing sound; at these times the prance may be viewed as the ritualization of leg-stamping.

The high-rise (A13) is characteristic of both sexes, unlike the preceding components of agonistic behavior. It represents the opposite of the creep, exaggerating as it does the size of the threatening crab. It reflects, once more, the importance of bigness as a signal in social behavior. In *Uca* males, as in other animals, the fact upon which it is based is that larger crabs in combat induce their opponents to go rapidly away more often than do smaller crabs. The high-rise is often combined with threat motions of the major cheliped. Unreceptive females performing a high-rise when approached by a male are often effective in deterring him without contact from an attempt to mate. Both sexes, but especially females, sometimes combine the high-rise with the acoustical signals of leg-wagging (S5).

It seems likely that the conflict during high-rises between tendencies to stay on the surface, feed, wave, or enter into combat, depending on circumstances, may be closely concerned in the origins of leg-wagging (S5). The motions are closely similar to those involved in true leg-cleaning. Displacement leg-cleaning is of frequent occurrence in such a situation, and the eventual development of acoustical equipment through ritualization of leg-cleaning appears to be a logical sequel.

The female's legs-out posture (A14) appears to be a special case of the high-rise (A13), indicating a stronger degree of rejection. Sometimes it, too, is associated with leg-wagging (S5).

All of the sound components now known appear to be primarily threatening in use, whether or not they are directly associated with an agonistic posture or motion, as often is true of the leg-wag (S5), as mentioned above, or with the threatening use of waving display. Only one of the group seems also to be a characteristic part of intensive courtship in a number of species; this is the major-manus-drum (S9); it is of course to be expected that others of the group are used in courtship underground or at night; Salmon & Atsaides (1968.2) considered leg-wagging in the evening at the surface to be a courtship signal in two species of *Minuca.*

Most of the components also crop up in ambiguous situations in the midst of waving display, when the displaying crab appears to have his attention divided between a female and either another male or an outside threat, such as an observer or camera close by. In these examples, the motions normally associated with sound components appear usually to be incomplete, and are therefore then to be classified as displacement activities. Feasible bases seem to be confined to cleaning and feeding motions. The major-merus-rub, minor-merus-rub, minor-claw-rub, palm-leg-rub, leg-wag, and leg-side-rub (S1-S6) seem to be more allied to cleaning, while the drumming of major and minor meri against the carapace (S7, S8) are possibly derived from feeding, and the minor-chela-tap (S10) more probably from the same source. No origin for the leg-stamp (S11) suggests itself. Bubbling (S12) and membrane vibration (S13) are both derived directly from respiratory processes by way, perhaps, of displacement behavior.

Special mention may be made of the minor-merus-drum (S8), which seems to be a good example of both apparent double ritualization and of ambivalent behavior. Whether or not the component was originally derived from feeding, the merus sometimes makes apparent drumming contact against some part of the suborbital region, although the sound has not yet been recorded; this occurs in threat situations only. In high-intensity waving display, however, *festae* and *lactea* sometimes shake the flexed minor cheliped in the air well in front of the suborbital region. This of course could be merely displacement minor-merus-drumming. At its most conspicuous, however, the minor cheliped is constrastingly lightened, and the motions seem to be an incorporated (though occasional) part of the high-intensity waving display; the shaking occurs in both courtship and threat, when no conflict seems to be involved. Under these conditions, it is a good illustration of the concept of ritualization.

(*c*) WAVING DISPLAY AND ASSOCIATED SOUND COMPONENTS

The first eight of the 14 motion components distinguished in waving display are characterized by movements of the major cheliped. Of these, the vertical-wave (W1) and the jerking-vertical-wave (W2) seem more likely to have evolved through ritualized displacement feeding than from any threat component, none of which is characterized by the strongly flexed cheliped shown in typical displays of *Deltuca*, in which social behavior is least complex (Fig. 87 *A*, *B*). It also seems likely that the vertical wave arose in at least some species through an intermediate acoustic element, the major-manus-drum (S9). In the wave-form shown in certain *Deltuca*, especially in *acuta*, the likelihood is clear. Additional suggestive examples are given in a few motion-picture close-ups, made with the camera on or near the ground. Here the major manus, although vibrating, does not reach the ground; nevertheless actual drumming is an integral part of waving display in the two examples, *saltitanta* and *deichmanni*, both of which belong to the socially advanced subgenus, *Celuca*. The occurrence of incomplete drumming in other species, when it is not a part of regular display, doubtless represents displacement drumming.

In contrast to vertical-waves, all waves with distinctly lateral, or obliquely lateral, characteristics seem clearly to have evolved from the basic threat posture of the lateral-stretch (A10). This derivation applies to the semi-unflexed-wave (W3), lateral-straight-wave (W4), lateral-circular-wave (W5), jerking-oblique-wave (W6), reversed-circular-wave (W7), and overhead-circling (W8). (Fig. 87 *C, D.*)

In many of the displays of many species, the classification of a wave-form as simply vertical or lateral would be inaccurate, even in unambiguous displays of high intensity, since the cheliped motions show characteristics of each, pushing slightly outward, obliquely upward, or both. Nevertheless the basic derivations even of such complex examples as jerking *Minuca* and the overhead circling of *maracoani* or *ornata*, when films are carefully analyzed, seem to have more in common with typical lateral wavers, their motions appearing more likely to be developments of warding-off threat gestures, than of feeding motions.

All jerking waves (W2, W6) appear unmistakably to be compound waves developed from simple waves, either vertical or obliquely lateral; each step in the ascent following the pause starts at the level where the preceding wave reached its peak, without or almost without descent.

The leg-stretch and prolonged leg-stretch (W9, W10) are both versions of the high-rise (A13) incorporated into waving display, without change in its function of increasing apparent size. The leg-wave (W12) is a clear example of a double ritualization, having come, it seems evident, straight through ritualization of the leg-wag (S5), which in turn seems equally obviously to have been derived from cleaning motions. In the field all stages of the sequence, including functional displacement motions in appropriate social situations, can sometimes be readily observed. The curtsy (W13), characteristic of high-intensity courtship in a number of species, apparently derives directly from an intention movement, with display and burrow descent tendencies in conflict. Salmon & Atsaides (1968.2) found it sometimes to be preceded in *Minuca* by the leg-stamp (S11).

The occasional incorporation of the minor-merus-drum (S8) into high-intensity waving display was described at the end of the preceding section.

(*d*) EVOLUTION OF CHIMNEYS, PILLARS, AND HOODS

The chimney, a wall closely surrounding the burrow, may have a double origin. The simplest derivation would be from bringing spoil from below, during excavation, and not tossing it to a distance. Such a heap, particularly after development into an encircling wall, would certainly serve to aid in keeping the burrow moist and cool, of special importance to ovigerous females. *U. urvillei*'s chimney is partly made in this manner.

Most chimneys, however, as mentioned earlier, are built through scraping mud from a distance of some inches, even though excavated mud is still carried or flung by the same crab to a similar distance.

The origin of this behavior must, it seems, be through a quite different pattern from that of excavation. The only likely activity seems to be the genus-wide habit of plugging the burrows with a stopper brought from some inches away. Since a similar function, in the same species and even individuals, is often performed by pushing mud up from below, it may well be that the origin of the wall is also double. It seems most unlikely that chimneys, prevalent in the less-specialized subgenera, have evolved from the highly specialized, rarely occurring, pillars and hoods, limited almost wholly to *Celuca*. The subgenus, it will be recalled, is the most specialized subgenus of all, both in adaptation to littoral life and in social behavior.

The sporadically occurring pillars and hoods are probably derived through phylogenetic simplification of chimneys. Each pillar or hood is made by bringing all material from beyond the burrow mouth; all differ strongly from chimneys in being built only by males during their display phases.

Salmon & Atsaides (1968.2) suggest plausibly that the structures may serve as amplifiers of acoustic signals. Still, if hoods are amplifiers they apparently do not serve for the amplification of sounds at night; there is no evidence that they are constructed during nocturnal low tides.

It also seems likely that pillars and hoods have arisen through ritualizations of chimneys, signaling to males the presence of a display territory and to females a potential mate. Possibly each structure represents, larger than life, the displaying male himself, visible outside the burrow to aggressive males and passing females even when he is not stretched to display height and even when he is underground.

Still farther out on the speculative limb is a suggestion which, if it proves experimentally to be valid, could be the most interesting explanation of all. In each of the species concerned, the female, when sufficiently stimulated, follows the male below ground. After the male vanishes, the only visual guide or stimulus for the female in the last several inches is the sight of the burrow—a dark object in the terrain. This is, of course, in addition to any acoustic signal the male may be making, or any stimulating effect of a previous visual image the female may retain.

It seems possible that if such a dark object is a releasing or directing mechanism, then a *vertical* dark object may be a better mechanism for attracting a female than one that is flat and foreshortened. In the highest development of hood-making, the structure fashioned by *musica terpsichores* alone is usually found on light-colored muddy sand; the shading resulting from the concavity would be an effective darkener.

Throughout the pillar-and-hood-making group, however, the principle appears the same. Setting a facsimile of the stimulus on edge makes it effective long before it would otherwise be clearly visible. Such a development would parallel the rising of a crab to dactyl-tip to wave. If the structure does stand for the hole, then it can be regarded as both a supernormal stimulus and a ritualized burrow mouth. A special sense for these terms is, then, needed, since the original stimulus, the hole, still exists.

Perhaps, finally, the structure functions in all three ways, amplifying sound, increasing the apparent size of the crab, and, ultimately, representing the burrow.

Unquestionably certain populations of pillar-makers are physically unable to fashion the structures because of inappropriate substrates. Nevertheless, the erratic appearance of pillar-building among and within populations remains mysterious. Possibly this activity is a case of genetically controlled behavior in polymorphic forms.

E. SUMMARY

The view is presented that in *Uca* the burrow has two chief functions—to provide shelter and, during the display phase of a male, to serve as the center of a defended area. These uses are termed *basic territoriality* and *display territoriality*. In this genus territoriality seems scarcely concerned with aiding the distribution of individuals in accordance with the food supply or of stabilizing their numbers. The principal function of combat may lie primarily in stimulating and synchronizing mating behavior, as well as in releasing tension during the reproductive period; combats often seem to progress for their own sake, particularly in highly ritualized mutual encounters. While in forceful fighting physical injury virtually never occurs, these combats are often prolonged. The behavior changes that sometimes follow combat are similar, whether the combat has been long and forceful or short and ritualized. Therefore the main advantage of ritualization in some species appears to be the shortening of combats, allowing more time both for waving display and for actual courtship. This interpretation is inadequate to explain the situation in other species, now under investigation; in these forms force itself is ritualized, forming a regular part of many combats; furthermore, during the course of a single period of low tide, combat and courtship are largely confined to different hours. In *Uca* basic threat postures provide defenses against predators, as in numerous other crabs; in addition the postures, motions, and acoustic signals have various signaling functions in both males and females; in intermale relations they often discourage contact of any kind, thus saving even more time than ritualized combat; they are commonly used in females to ward off unacceptable males, as well as in occasional interfemale encounters. Threat postures and acoustic signals also may well prove to have stimulating value, both to the actor and to conspecifics. In waving display most of the components are employed both in intermale situations and in pure courtship; a very few occur only in high intensity courtship. It seems certain that waving display serves as an identification mark, treated variously by conspecifics, depending on sex, physiological stage, and age; and that it is stimulating at least to females. Probably it also stimulates males; by repelling most other males it can in addition avoid the time needed even for threat postures. Interspecific differences in waving patterns discourage incompatible courtships among closely related species. The burrow of a waving crab, as well as any structure beside it, may be viewed as an artifact of display. Displacement behavior is discussed. A speculative review follows of the likely derivations of the principal components of combat, threat, waving display, and their associated sound components through the ritualization of fighting, withdrawal, feeding, cleaning, and respiratory activities. The derivation appears often to be through the medium of displacement activities, as well as, in waving display, from threat postures. The more specialized structures beside the burrows of some displaying crabs are probably derived from moisture-conserving chimneys that occur rather widely in the genus; their functions during display may amplify sound, increase the apparent size of the crab and possibly represent the burrow. The need for physiological research is stressed in several sections.

Chapter 7. Speciation, Phylogeny, and Directions of Evolution

OUTLINE

A. INTRODUCTION

In *Uca* the evidence on evolutionary trends remains indirect. Fossils are confined to three specimens, one of them a dactyl, while in related groups they are similarly rare. Genetics is untapped. Even the indirect evidence is restricted, since our knowledge of comparative development, basic physiology, sense organs, and neurophysiology is rudimentary or wanting. Experimental work on behavior is starting, but has scarcely begun to extend to the comparative approach; only several releasers have been studied experimentally.

On the other hand, both morphology and behavior have yielded information of aid in working out the probabilities of fiddler crab descent. Wide distribution, diverse habitats, numerous forms, and social complexities all invite comparative studies. Many of the results now at hand combine to give persuasive evidence on the group's development.

On the basis of present knowledge, then, the following pages will discuss roots of speciation and directions of evolution in *Uca.* With material from earlier chapters, connections among the subjects will be stressed. The chief of these relationships are outstanding features of morphology and behavior to each other, as well as to certain aspects of distribution and ecology. The principal viewpoints are the extent of variability, the role of allopatry, and the adaptations related to sympatry. Stimuli to evolution and rates of change are considered. A phylogeny of the group is proposed. Finally a brief discussion comments on directions of evolution within the group.

References are largely omitted in this chapter, since it is based on material presented in the systematic section (Part One), discussed in the preceding chapters of Part Two, and included in the indexes. General references to zoogeography, ecology, and behavior appear in the introductory sections and subsections of the pertinent chapters. Documented discussions of allopatry, sympatry, and related topics are given, in particular, by Grant (1963) and by Mayr (1963, 1970).

B. PLASTICITY

The chief characteristics of *Uca* can usefully be viewed in two groups, one including the conservative essentials of maintenance and the other the diverse features connected with reproduction.

Adaptations in the first group deal with the individual's basic needs as an amphibious, filter-feeding crab that lives its entire adult life in the intertidal zone. They control respiration under fluctuating conditions, help retain moisture, extract nourishment from the substrate, promote efficient movement out of water, and, through vision, vibration receptors, and burrowing behavior, provide means of escape from predators. All of these functions take place in a complex of rhythms controlled at the least by light, tide, and seasons. The extremes of ecology to which fiddler crabs are exposed are nonetheless limited and repetitious; their related adaptations are therefore as a whole conservative. For this reason the structure of the gills and mouthparts, for example, have limited usefulness in tracing the evolution of the group, although some of the details are clearly responsive to ecological needs. Similarly, the general shapes of the carapace differ little, all species being roughly four-sided and slightly broader than long, as are numerous grapsoids; the eyes are always erectile on definite stalks; the ambulatories show only modest ranges in shape and length. Behavior patterns associated with maintenance vary even less; walking, digging, and feeding motions are virtually identical in all fiddler crabs.

Most physiological characteristics in *Uca* have not yet been examined from a comparative point of view. Some topics are beginning to furnish rewarding data in relation to ecology; these include species-specific tolerances to temperature, salinity, and drought, as well as differing requirements in food. All of these factors, vital as they are to an understanding of evolution, depend on characters which for the practicing taxonomist are now largely cryptic and for the evolutionary biologist still too little known to be related to his information from other disciplines.

The second group, ultimately concerned with reproduction, includes the most striking characteristics of appearance and behavior in fiddler crabs. Often they prove useful in showing relationships among subgenera, species, or both. In morphology the principal characters are connected with the shape and armature of the major cheliped, the armature of the orbits and ambulatories, and the shape of the gonopod tip. Since parallelism and convergence are extremely common in gonopods, these appendages must be used with particular caution as phylogenetic clues. In behavior the chief variables are the waving patterns of the major cheliped along with associated movements of other appendages, a few components of combat and threat, the two basic forms of the behavior of females during courtship, and the shapes of any structures fashioned beside the burrows. In different categories of social behavior are the relative amounts of time devoted to waving display, the peak hours of social activity, and the prevalence of displacement activities. All these forms of social behavior are under the control of at least two internal rhythms, which are in turn partly associated with the ecologic rhythms listed above. One of these internal rhythms is connected with the state of the gonads; the other is controlled by short, physiological phases. Both groups of rhythms show some differences within the genus, although little information is as yet available.

One characteristic that should be specially mentioned is the sporadic occurrence in *Uca* of a species or subspecies that differs strikingly from its close relations in gonopod morphology or waving display. As will be shown in the section on sympatry, the evolutionary pressure for the peculiarities seems clearly to be the maintenance of barriers among forms that are sometimes sympatric. The point to emphasize here is that the tendencies toward startling change are in themselves definite attributes of a subgenus or a species.

Two morphological characters related to each other definitely differ among some subgenera, and are hence of basic taxonomic usefulness and potential evolutionary interest. These are the breadth of the front and the lengths of the eyestalks. Unfortunately functional reasons for these differences remain puzzling.

C. ALLOPATRY

As in other advanced groups of animals with many surviving species, forms of *Uca* with different ranges often seem clearly to have developed from common ancestors. Sometimes their differences from one another warrant specific status, their relations being indicated in this contribution by their grouping into the informal category of superspecies. Sometimes the differences appear to require only subspecific status. Again, certain populations show very minor and variable differences, which either are too poorly known to justify the proposal of a subspecific name, or else the atypical traits appear sporadically in other parts of the species range.

The strength of these tendencies to differ geographically varies with the terrain. Along the unbroken coasts of Africa and the warmer parts of America, the allopatric splitting appears to have been less than on the fragmented shores of southeast Asia and the adjacent seas.

For example, no overt differences exist between populations of *Uca* in the Red Sea and those in Mozambique that make desirable the proposal of subspecies. Although some individuals in the more southern populations of *lactea annulipes* show minute differences in claw proportions, these distinctions are minimal in comparison with geographic distinctions in this species that center in the Sunda region to the east. Similarly, along the entire coast of west Africa none of the forms into which *tangeri* has been occasionally divided appears to be justified.

In the western Atlantic, other examples give more scope for discussion. Two species range from Florida or the Bahamas to southern Brazil, while five more occur from the West Indies to Rio de Janeiro. None of them seems to me to give valid grounds for the erection of subspecies. Yet the direction of the equatorial current in the northeast part of the bulge of Brazil is westward, the counter-equatorial current chancy, and the drought-ridden dunes of the region inhospitable to fiddler crabs. It may be of course that differentiating traits within species on continuous warm coasts are chiefly physiological, as we are finding is true of temperate forms in the United States (p. 441). If so, these cryptic characters contrast with the morphological and ethological traits which are conspicuous whenever allopatric forms are given taxonomic recognition and which, in the considered forms, suit a variety of habitats.

More probably, the widest-ranging species of the Americas and Africa do owe their homogeneity, as first suggested, to the simple fact of the continuities of the coasts and to their relative stability. Even along the barren shores of northeast Brazil a few havens offer refuge, breaks in the dunes to streams behind. Spring tides and rare rains carry megalopa shoreward and infrequently bring hatchlings to the open sea.

In the heart of the Indo-Pacific region, in contrast, well-marked subspecies are the rule. This condition may be due to the lower hardiness of Indo-Pacific larvae under adverse conditions or to shorter development periods. Yet these suggestions seem unlikely. Rather, the explanation must lie partly in the sheer prevalence of islands and of broken coastlines, as well as in the distances between landfalls. Finally, beyond these possible aids to subdivision, the key stimuli have certainly been the temporary isolations of a continuing volcanic past.

The characteristics of marginal populations in wide-ranging species of *Uca* have not yet been compared in detail with those of populations of the same species that are more centrally located. Nevertheless it is already clear that the outpost groups show no striking tendencies to differentiation. Apparent reasons for their continuing similarities to the central stocks differ in species that range widely from west to east from those with distributions extending far to the north.

Longitudinally, the only examples of marginal populations are *tetragonon* and *chlorophthalmus.* These two species alone reach mid-Pacific. In this tropical climate, on the western edge of the Eastern Pacific Barrier, and with the major currents directed back westward, these populations might be expected to show at least tendencies to subspeciation. Such is not the case. The survival efficiency of their larvae is probably formidable and may be the key factor in keeping open the gene pool of these most oceanic of *Uca.* It also seems likely that at least the westward counter-equatorial current may be a thoroughfare.

In populations of *Uca* at the latitudinal extremes of species ranges, accommodation to cold is the usual problem, and there is continuity with populations from warmer waters. Evolution here may well be lethargic because of the few generations possible, compared with the nearly continuous breeding found in wet tropical regions.

The topic of mingled populations of allopatric forms is crucial to any survey of evolution in the genus. In a few cases these overlapping boundaries between allopatric species and between subspecies are strikingly apparent. Viewed pragmatically, the populations are of course sympatric in the most restricted sense of the word. They will therefore be considered in the next section.

D. SYMPATRY

(Figs. 92, 93)

Twenty years ago the genus *Uca* appeared to be crowded with forms confusingly similar yet occurring in the same places and showing no evidence of interbreeding. Accordingly, they seemed to meet the criterion of species status, "sympatric coexistence without interbreeding," although their numbers appeared excessive even for a group as diversified as fiddler crabs.

Field work, reviews of the literature, and the study of museum collections have now somewhat reduced the problem. Potentially sympatric species of *Uca* turned out to be of four kinds. Some, recorded from a single locality, proved to occur as adults in distinct habitats. Many other records indicating sympatric occurrences were based on taxonomic confusions. In a third group, juveniles were described or identified as different species from the adults. Finally, many forms reported from the same place do in fact coexist in perfect sympatry, two or more species of great similarity mingling on the same strip of shore. The members of this final group are the subjects of this section.

The geographic barriers which led eventually to instances of sympatry are occasionally apparent. Examples are the repeated topographical changes in southeast Asia and emergences of Panama. In particular, the common ancestors of the superspecies *acuta* and of *dussumieri* in the Tethys area may well have been temporarily separated merely by an earlier version of the Sunda Shelf. After its submergence, the species held distinct. Still later they subdivided, through reemergence of the land, to varying degrees that still persist. Nevertheless in most cases of sympatry among very closely related forms the origins of the situation are so uncertain that speculation is unrewarding.

As Mayr illustrates in the course of his discussion of sympatry (1963: 449ff.), when similar species in any group become better known, biologically and morphologically, differences between them turn out to be numerous. In *Uca* no instances appear of the infrequent, anomalous sort of which an example is the *pipiens* group of *Culex.* Always, when we have enough information, these morphologically similar fiddler crabs prove to be distinct in assorted structural and behavioral characters. Usually the preferred microhabitats also differ.

As in other animals a number of conditions appear to have been prerequisites for sympatry. These are, first, a period of geographic isolation, during which differentiation of two or more forms became genetically fixed; second, removal of the barriers; third, migration into areas of competition; fourth, additional adaptations to food or substrate as needed to permit geographic coexistence; fifth, adjustment of reproductive morphology, physiology, and mating behavior in such ways that productive matings are promoted, wasted germ cells avoided, and so, incidentally, specific barriers maintained.

In *Uca* the disadvantage of wasting time is probably still another factor in the evolution of distinctive mating patterns. Because of the limited intertidal hours available for courtship, behavior that discourages the attraction of unsuitable partners should have positive value.

The morphological characters that usually aid most dependably in distinguishing species that are closely sympatric are the tip of the gonopod and, sometimes, the form of the female's gonopore. Behaviorly two such species almost always are strikingly distinct in their waving displays. Sound probably will prove also to differ significantly among sympatric forms. Almost certainly chemical factors provide the remaining principal barriers, but they have not been explored.

Differences in habitat preferences, while often pronounced, are at best inefficient dividers between *Uca.* Even species normally found in distinct biotopes often intermingle both in areas rich in nourishment and along adjacent margins of their preferred niches. Differences in breeding seasons, which in many other animals form important barriers, are almost nonexistent in *Uca.*

A final point of interest concerns the increasingly apparent tendency of species to differentiate locally in waving display, gonopod form, or both, in such a way that their characteristics become distinct in relation to the species most closely related to them with which they are sometimes sympatric. The principle is known in certain birds and other animals when allopatric forms occur together in boundary zones. Here their differentiating characteristics are often more pronounced than in parts of the ranges where the two forms are not in contact.

Nevertheless, the similar phenomenon in *Uca* appears more complex, since characters which would be viewed ordinarily as of specific or at least subspecific importance if a restricted part of the range were examined prove themselves to be highly plastic. It was only when the differing sympatric associates of certain allopatric populations were considered that the sometimes abrupt differences began to be understandable, as the following examples will suggest.

The occurrence of jerking in the waving displays of the superspecies coarctata *and the species* dussumieri. In the Indo-Pacific the most widely ranging allopatric *Uca* is the informal superspecies *coarctata.* Found from east Africa to Fiji and Japan, it is divided formally in this study into four species, one of which is subdivided into two subspecies. Table 23 shows these divisions, their ranges, and the waving characteristics under consideration, along with those of their closest sympatric relations. Figure 90 presents the displays of two of the subspecies in diagrammatic form, for comparison with those of the species sympatric with them. With two exceptions the members of the superspecies are the only jerkers in the observed sympatric assemblies. In one exception both *forcipata* and *rosea* proved to be jerkers, although their rhythm, as far as could be determined from insufficient observation on *rosea,* is quite different. The second exception concerns populations of *c. coarctata* that are regularly intermingled in the Philippines with *d. dussumieri*—a close relation of similar size and appearance. Here both *coarctata* and, in a complete change of its own usual pattern, *dussumieri* jerk vigorously. The display of *coarctata,* however, is fully distinguished by a series of forceful diminishing waves that follows each jerking primary wave; the diminishing waves are of greater amplitude, and hence more conspicuous, than in populations in Fiji, where *dussumieri* does not occur, or in northwest Australia, where *dussumieri* does not jerk. In all of these pairs of Indo-Pacific forms the gonopods are distinct.

In Indo-Pacific narrow-fronts, it will be recalled, mating is sometimes not prefaced by waving display, although the male is always in a waving phase during the low-tide period concerned. Also, the female is approached close to her own burrow by the male, instead of attracted to his; when unreceptive, she either assumes one of the appropriate threat postures or simply goes underground down a shaft, which is usually too small for the male to use. Thus, the importance of waving display in courtship and as a species barrier is more questionable than in the socially advanced subgenera. Yet the example of sympatric differences just given indicates a value to the species of waving display that is more directly concerned with particular potential copulations than with any of the other functions of this behavior that have been postulated (p. 517).

Local display differences among forms with similar gonopods. In *Minuca* of the eastern United States an evolutionary situation of great interest is becoming apparent, through the work of Salmon (1967) and of Salmon & Atsaides (1968.1, 1968.2). The species most concerned are *rapax,* its northern allopatric representative, *pugnax,* and two related forms on the Gulf of Mexico, described by Salmon & Atsaides as species and viewed here as subspecies (p. 190). Of major interest is the observation that Atlantic coast populations of *pugnax* differ in the distinctness of the jerks in their waving display. Once more the explanation seems to lie in their sympatric associations. Where the ranges of *rapax* and *pugnax* coincide in eastern Florida, the jerking of *pugnax* is absent, while that of *rapax* is as pronounced as usual. Farther north, *pugnax* jerks are distinct, indicating that this very common component of waving in many *Minuca* has been weakened in the coincident area under the pressure of sympatry. Differences of similar interest, including both speed of waving and acoustic characters, exist among the forms occurring sympatrically along the Gulf coast.

It is noteworthy, in view of these behavioral differences, that in *Minuca* the gonopods of groups of closely related species, even where these regularly occur sympatrically, are so similar that they are often of little taxonomic use. This is particularly true since individuals even within populations show considerable variation in the one or two details, such as the degree of flange projection, that might be helpful. We may expect more cases of clear behavioral distinctions to come to light in this group where gonopod differences appear to be so slight.

Regional hypertrophy of gonopod characteristics. Throughout practically all the rest of the genus the gonopods are specifically distinct and, on the taxonomic level, thoroughly reliable. Intraspecific variation is minimal and confined to such non-functional parts as vestigial thumbs. Gonopods are also one of the best indicators of phylogenetic relationships within the group.

Yet in an Indo-Pacific species, *vocans*, allopatric populations show such exaggerated and contorted variations of their parts that in any other instance these differences would be considered excellent taxonomic characters for defining full species. All other morphological and display characteristics, including the rather conservative gonopores of the females, show at most characters of subspecific value, while in colors and ecological niches all the allopatric forms are closely similar. Finally, apparent hybrids occur in New Guinea and the Philippines (Table 3). To consider these forms full species would certainly be unwarranted.

The explanation for the development of these gonopod distinctions seems once more to lie in the sympatric associates of *vocans*. The species shares virtually all of its range with *tetragonon*, a member of the same subgenus with a more conservative gonopod; *tetragonon* is usually found in more exposed locations and shows no definite regional variations from Africa to the Tuamotus. Occasionally the two species are locally closely sympatric. *U. vocans*, however, appears regularly to extend its range farther north than does *tetragonon* and the gonopod of this northern subspecies approaches the simplicity found in *tetragonon*.

The sympatric crowding in the Philippines appears responsible in *vocans* for the opposite effect. Here the local subspecies often associates with from one to five species of the neighboring subgenus *Deltuca*, each of which has a gonopod of basic design similar to that of *tetragonon* and *vocans*. On these shores the gonopod of *vocans* attains its most contorted form.

There seems to be no question but that in the even more crowded parts of the eastern Pacific similar explanations will be found for some of the abrupt shifts in gonopod form characteristic of the subgenus *Celuca*, where the change from flanged to tubular gonopods and perhaps back again has apparently occurred several times.

In a wholly American group, the subgenus *Uca*, occurs an example of gonopod differences with so few species involved that the evolutionary pressures appear clear. These species are clearly related to the Indo-Pacific *vocans*. Several of the group of six have gonopods recognizably similar to the old Indo-Pacific pattern, as well as to *tangeri* in the eastern Atlantic and, of course, to one another. In the remainder of the subgenus, including their allopatric members on opposite sides of the Panamanian isthmus, the gonopods when considered alone appear to belong to unrelated forms. Included is an Atlantic species, *major*, in which these organs are flangeless, thumbless, and tubular, while their Pacific counterparts, as well as *major*'s occasional sympatric, *maracoani*, have opposite characteristics of a wholly conservative nature. Again, the likely explanation for the striking difference appears to be the sympatric association.

E. STIMULI TO SPECIATION AND RATES OF CHANGE

Probably the greatest single stimulus to evolution in *Uca* was the presence of suitable habitats in America that were incompletely occupied by animals of similar needs, or by animals that succumbed to new competition. Here the postulated migrants across the Behring Bridge during the early Tertiary could flourish in the necessary isolation. Under such conditions a consequent burst of speciation would not be surprising. A somewhat similar stimulus was the blocking off of the Indian Ocean from the Pacific by the Sunda and, probably, Sahuli Shelves. These events, repeated a number of times to various degrees of completeness, gave recurrent spells of isolation. A third stimulus, comparable to the second, was the emergence of the Isthmus of Panama, most recently about five million years ago. A final impetus occurred more recently in the Philippines and East Indies; during the orogenic activity of the late Cenozoic, species probably evolved rapidly with the appearance of temporary barriers and rich new land.

These four events give some idea of evolutionary rates within the genus.

If the hypothesis of Behring migrations in the early Tertiary is accepted, along with the corollary that two Indo-Pacific *Uca* came from American stock, then four American subgenera, totaling 45 species, developed during some 30 to 55 million years. These totals comprise almost half the subgenera and more than two-thirds of the known species, including all those that are most specialized for littoral life morphologically and most advanced in the development of social behavior. The specializations and developments unique to the American subgenera (and to *tangeri*, its one eastern Atlantic derivative), include the following: enlargement of branchial chambers; maxilliped adaptations for dealing with food particles sifted in partly dry, muddy sand rather than in wet mud or sandy mud; development of the lateral-circular-wave; development of male-fashioned pillars and hoods; development of the female's following of the male, leading to copulation beneath the surface; and development of special acoustic signaling and combat components that do not apparently occur in Indo-Pacific subgenera.

The last closing of a seaway through Central America near the end of the Pliocene gives us our most exactly known date for the beginning of a period of complete isolation in *Uca*. This land barrier last became entire perhaps five million years ago. There is no indication whatever that larvae, much less adults, have migrated through the Panama Canal.

During these past five million years five pairs of Pacific-Atlantic allopatric species have evolved; the 10 species total one-quarter of all American forms considered in this publication to hold specific rank. In three other species the allopatric populations are so similar that, for consistency's sake, the members of both pairs have been designated subspecies. Most of the east–west allopatrics however differ in major characteristics of gonopods, gonopores, cheliped ridges, and pattern of waving display, the distinctions being clearly on the specific level.

Unfortunately, the duration of the Sunda barrier is uncertain. Similarly uncertain is the length of time during which took place the major orogenic activity in the islands to the east and south of Sunda. Nevertheless, it is fairly well agreed that the old Sunda barrier broke down very recently, perhaps within the last 10,000 years. Since then there has been freedom of mingling, so that it is possible to determine how fixed had become the reproductive barriers among the allopatric forms fostered by the presence of the Sunda Shelf.

Without exception, only minor morphological and behavioral differences evolved during the short period of isolation. For example, structural changes show best in the size of gonopod flanges and degree of torsion; in the shape and modeling of the front; minor differences in the suborbital system of tubercles and ridges; ill-fixed, small changes in the tuberculation of the prehensile edges of the claws. In behavior the differences, confined chiefly as usual to waving display, are even slighter, comprising distinctions in the prevalence of jerking, or of seriality in the waves; there are also sometimes stronger or weaker tendencies to build chimneys or pillars. In four species these differences are considered to be on the subspecific level, particularly in view of evidence of interbreeding where populations coincide; in two superspecies the differences are here regarded as of specific importance. As usual in such cases, an argument could almost as easily be made for considering even these superspecies as species composed of particularly distinct subspecies, in which no evidence of interbreeding has been found. (See Tables 2, 3, 6, 22, and 23, along with the associated portions of the text.)

F. Phylogeny

(Figs. 96-101)

The distinctness of *Uca* as a genus has been mentioned several times in these pages. *Ocypode* is generally agreed to be its closest relation. Yet the basic differences are numerous and no intermediate forms remain.

Uca itself, in contrast, is composed of a wealth of radiating species, many of them closely related and some of these intermediate between groups. Nevertheless, in spite of difficulties, the genus does divide into categories which are very distinct, when end forms are compared. For evolutionary studies it is fortunate that corresponding ecological niches exist in the Indo-Pacific and in America. By comparing adaptations in the two hemispheres, it is possible to separate similarities indicating relationships from those which probably represent ecological parallelisms and convergences. By this means hypothetical ancestors and evolutionary trends can be suggested.

With this background in mind, then, what were the probable characteristics of ancestral *Uca*?

It seems that this crab must have been only moderately specialized for an amphibious life or for a particular substrate. Its waving display was a simple vertical raising and lowering of both flexed chelipeds, as in various grapsids and ocypodids, as well as in the *Uca* subgenus *Deltuca*. Both visual and acoustical displays were used, but only in basic territoriality and intermale relationships, and little or not at all in courtship. Forceful combat certainly existed, since it is prevalent in decapods, and probably also, as in some other crabs, simple forms of ritualized encounters. The gill system was well developed. The front was moderately narrow. The gonopod was of the basic type, with well-developed flanges and with the broad inner process found in various ocypodid genera as in most members of *Deltuca*, *Thalassuca*, and *Minuca*.

The *Uca* living today that are most similar to this hypothetical ancestor comprise the Indo-Pacific subgenera *Deltuca* and *Australuca*. Their patterns and armature of social behavior are less highly developed than in the other groups. In general they specialized for mud-living through a number of devices that seem to facilitate the drainage of liquid mud from carapace and appendages. The lower margins of the orbits are rolled out, while the suborbital crenellations, always easily clogged, are low and the series short. The eyestalks fit loosely in wide sockets. Before the use of cheliped armature was observed in the combats of American crabs, it seemed to me that the function of chela grooves in Indo-Pacific forms must also be to aid in drainage; that potential use now seems more dubious but still undetermined. The small chelae on mud-dwellers are all well toothed, preventing moist mud from sieving through the gape on the way to the mouth. Ambulatories are usually broadened, perhaps originally only as a hindrance to sinking in deep mud, but at least at present thus affording an increased area for stridulatory armature. In females throughout the genus the ambulatories are more frequently broadened and to a greater degree, perhaps in adaptation both to the female's carrying heavy eggs and to her spending much of her ovigerous period in very wet areas, near the tide's edge; the broadening also provides space for additional stridulatory armature, also better developed in females as elsewhere in the genus, her threat and combat components being largely restricted to activities of the ambulatories. Display whitening does not occur in *Deltuca* and *Australuca.* Certain colors, particularly in the young, are often striking; carapace spots of blue and red or white in adults have given some evidence of use in threat postures.

In social behavior species of *Australuca* are slightly more advanced than those of *Deltuca*; they spend more time in waving display, the wave is of somewhat greater amplitude, and courtship shows the beginning of complexities. In particular, a male sometimes herds a female toward his own burrow, pushes her down it, and then follows.

In contrast to the foregoing mud-livers, another Indo-Pacific subgenus, *Thalassuca*, is adapted to relatively exposed marine habitats—muddy sand near low-tide levels, shell-encrusted rocks and dead coral in even more exposed localities, and pelagic islands. Specializations have perhaps included a longer larval period, or at least a period capable of prolongation. These crabs lack most of the apparent adaptations for mud-living. The orbits are not rolled outward; the crenellations are well formed and extensive, appearing equally suitable for water drainage and for stridulation. Grooves on the major chela are reduced or absent. The small chela gapes more and has smaller teeth, since the gobbets of food-bearing substrate, large but sandy, apparently are thus brought more efficiently to the mouth in the setigerous tips of the chelae. Unlike the situation in *Deltuca*, copulation is always preceded by waving display, which, however, remains almost purely vertical and without complexities. *Thalassuca* spends far more time in waving display even than *Australuca.*

From close to the base of *Thalassuca* probably came *Amphiuca* (*chlorophthalmus* and *inversa*). The two groups show affinities in their third maxilliped gills and in the presence of an accentuated depression, almost certainly of importance in combat, on the outer pollex base. They differ markedly in the gonopods which, as in aberrant *Deltuca*, have lost or modified the flanges, reduced the inner process, and, in *chlorophthalmus*, elongated the tip into a projecting tube; similar changes in gonopod structure happen sporadically in the subgenus *Celuca.* They differ also in the wider front, smoothness of the manus, and in more distinct traces of an incipient lateral wave than in any other Indo-Pacific subgenus.

Except for the broad front and the wave, *chlorophthalmus* and *inversa* show clearly their less-specialized origins. The wave is still altogether in a single plane and without circularity, in spite of its partial laterality. Again, the male still approaches the female and mates on the surface. It is interesting, in view of the hypothetical origin of American forms developed below, that *chlorophthalmus* females in breeding condition build chimneys, as do both some *Deltuca* in the Indo-Pacific and some *Minuca* in America. *Thalassuca*, on the other hand, build no structures whatever. Like *Thalassuca, chlorophthalmus* is an adaptable colonizer, and in mid-Pacific is found on poorly protected shores; *inversa*, in contrast, builds no structures and is confined to protected flats in the extreme western part of the Indo-Pacific.

It seems likely that American groups developed from one or more stocks ancestral at least to *Thalassuca* and probably to *Amphiuca.* From such a base the present-day American subgenera could all logically have developed, including *Uca*, *Minuca*, *Boboruca*, and *Celuca.*

All of these, along with *Afruca* (*tangeri*), show such similar elaborations of social behavior that it seems they must have a common basis. These elaborations consist of the following patterns: the attraction of the female to the burrow of the male, with mating underground; the development of a circular lateral wave widely used in high-intensity display; the frequent use of the mero-carpal joint, lower side of the manus, and pollex of the major cheliped in drumming on the ground; and the sporadic use of curtsies in the final stages of courtship. With the possible exception of ground-drumming, none of these specializations occurs in *Deltuca*, *Australuca*, *Thalassuca*, or *Amphiuca*, all of which are restricted to the Indo-Pacific.

Beyond these similarities, however, the American subgenera differ in outstanding particulars when intermediate forms are disregarded. *Uca* and its relation, *Afruca*, are closest to the original stock of *Thalassuca*. Their basic similarities comprise gonopod structure, including the tendency of those appendages to striking exaggerations and differences among related forms; carapace and cheliped shape; gill structure of the third maxilliped; and the basic form of display with the lateral circular element usually weak. When in fact a *heteropleura* (subgenus *Uca*) is waving on a shore in Panama he bears a striking resemblance, even in color, to a *vocans* (*Thalassuca*) on the other side of the Pacific. Nevertheless his is strictly an American design, having, in addition to the *Thalassuca* resemblances, all the characteristics listed in the preceding paragraph.

As a whole, the closely related members of *Minuca* are mud-dwellers and correspond ecologically to *Deltuca* in the Indo-Pacific. Their gonopods are of the conservative ocypodid type found in most *Deltuca* and all *Thalassuca*, with flanges and inner process well developed, unlike *Australuca* and *Amphiuca* in the Indo-Pacific. Chimney-making, a pattern often found in Indo-Pacific mud-dwellers far back on protected shores, is prevalent in *Minuca* too; it may prove to be chiefly a superficial similarity, resulting from equivalent ecologies. Its drainage arrangements apparently depend on short sockets, smoother appendages, and slender chelae, rather than on rolled-out orbits, and, perhaps, the channeling aid of grooves on the claw. The broadening of the front reaches its maximum in *Minuca* and remains unexplained. It may be nothing more than an incidental effect of orbit shortening, resulting in faster cleaning. Yet it seems unlikely that this adaptation would have evolved along with necessarily shortened eyestalks, reducing the field of vision. The slender stalks found in Indo-Pacific groups and accentuated in the subgenus *Uca* would, it seems, have proved a less expensive cleaning system. Perhaps a broad front, simply but importantly, adds space for neural connections. Finally, *Minuca* is especially notable for adapting better and more frequently than any other group to extremes of drought and cold, through aestivation and hibernation.

The subgenus *Boboruca*, erected for the Atlantic and Pacific allopatric forms of *thayeri*, in some ways resembles *Deltuca* more closely than do any of the other American subgenera. The similarities lie in the shape of front and carapace and in its social behavior; yet its armature is characteristic of American forms. As a whole it appears to be merely a conservative descendent of one of the postulated migrants, rather than a more direct representative of an Indo-Pacific group. The fact that the Atlantic and Pacific populations have changed so little since the isthmus last emerged further supports this interpretation.

Except for mud-living adaptations, most specializations reach their height in *Celuca*. Waving display is elaborate, with a great increase in waving speed and in the time devoted to it; morphological specializations for ritualized combat are most numerous; structures beside the burrow, built only by displaying males, appear sporadically among the species. In *Celuca* also occurs the highest toleration of exposure to air; the equipment to extract nourishment from a relatively sandy substrate; the greatest elongation of walking legs, providing relative speed in movement on the ground; the greatest elongation of the claw, and (along with several members of the subgenera *Uca* and *Thalassuca*) the prevalence in end-forms of highly developed display-whitening. Finally, one characteristic making possible the explosive evolution of *Celuca* in the eastern Pacific has certainly been their small size.

This is the only American subgenus to occur also in the Indo-Pacific, where it is represented by two species. One of them, *lactea*, is not only the widest-ranging *Celuca* but one of the most successful species in the entire genus.

G. DIRECTIONS OF EVOLUTION

Fiddler crabs have specialized in three principal directions. Almost all of their outstanding peculiarities now seem rather clearly to indicate these trends. The first leads toward a more terrestrial environment, the second toward the sharing of habitats by closely related forms, and the third toward sociality. These trends appear not only when the genus is viewed as a whole but within the larger subgenera.

Adaptations toward a more terrestrial environment. Modern *Uca* are already well adapted to intertidal life. All can withstand exposure to the air, all can move efficiently in that thin medium, and all feed during low tide by sifting the substrate. Furthermore, all use burrows efficiently as protection from desiccation and predators, while all depend on vision and substrate vibration as warning systems.

Within the group only the adaptations to life out of water and to sifting substrate show notable differences. Repeatedly the phylogenetic trend has been to move to higher levels of the littoral that are uncovered for longer periods, or to colonize flats that are flooded only intermittently. In both these situations even the bottoms of the burrows are sometimes dry; moisture conservation then becomes of prime importance. The most obvious structural adaptation of these species is the increased volume of the carapace, attained through arching in all dimensions. A similar response is found in the several hibernating species.

The second obvious adaptation of many species living higher on the shore is the development of specialized setae on the mouthparts. These setae, found in species on somewhat sandy, sloping biotopes, are shaped for rubbing off food particles clinging to the grains of sand. Simpler setae strain out organic matter from the finer silt of more muddy levels.

Adaptations to sympatry. Although coastlines are impressive in mileage, their area is negligible compared with those of other habitats on sea and land. And of all the stretches of climatically suitable shore, only a few offer support to *Uca* and fewer still provide abundant food. It is in such favored places that *Uca* congregate. This sharing of rich and restricted biotopes by related forms requires both that food supplies remain adequate and that species barriers be maintained. Fiddler crabs have dealt with the first requirement partly by miniaturization. This solution shows supremely well in the sympatric associations of *Celuca* in the tropical eastern Pacific and, less strikingly, of *Deltuca* in the Philippines. Adjacent or coincident microniches with differing foods will doubtless also prove to be of major importance for sympatry. In these favored localities genetic barriers are reinforced principally by differences in waving display, form of gonopod, or both; color and acoustic behavior will probably be found to be of secondary importance.

Adaptations to increased sociality. The trend toward sociality appears closely related to the first trend mentioned—that toward a more terrestrial environment. Throughout the genus the species living closest to low-tide levels devote less time to waving display during each daytime low; an obvious explanation is that there is not enough time both to feed sufficiently and to display at length. Although this conclusion is probably sound, it does not cover the general principle that in the less social subgenera, in particular most *Deltuca,* waving display is largely confined to a few days every two weeks; in socially advanced groups the restriction is far less rigid. Since the upper levels are nearly always less rich in food than the lower, the upward migrations of breeding males in socially advanced species solve the time problem at the expense of convenient food; it will be remembered that these males feed relatively little during their display phases, apparently making up for their fasting during other parts of their cycle.

In all these advanced subgenera the males not only seek out higher, more open, or conspicuous territories and wave for longer periods but share additional social characters. Their attachment to particular territories is more sustained; their high-intensity waving display is faster, more complex, or both; display color change in three subgenera is often striking; mating is normally underground instead of on the surface, with the female attracted to the male; the morphological specializations for stridulation and ritualized combat reach their apex; displacement behavior is prevalent. All of these developments become most elaborate in end-forms of *Celuca,* although in some *Uca* and *Minuca* similar complexities are achieved. In short, the trend is to make social behavior more active, more time-consuming, and more complex.

The development of species-specific social behavior makes possible the full use of coincident and adjacent niches by closely similar forms. Behavioral diversity makes the crowding possible and probably contributes, in a literal feedback mechanism, to the richness and attractiveness of the environment. The results of crowding by individuals and species are not only probable enrichment, for *Uca,* of the substrate through glandular and other contributions. They also provide the social stimulus of active animals.

The high value of social behavior to *Uca* is strongly indicated by the eastern Atlantic species, *tangeri.* With the possible exception of rare strays from unrelated subgenera, this fiddler crab shares the coast with no other *Uca.* Yet, in spite of a total lack of sympatric associations, it maintains intact a large and highly evolved repertoire of social components.

We do not know with any certainty the advantages to *Uca* that these varied components provide. Only a few are fairly apparent when direct courtship behavior is observed; here the activities are comparable to those of courtship in many other animals.

On the other hand the emphasis on combat—its prevalence, patterns, and equipment—remains a puzzle. It is all very well to toss off the whole astonishing production as a mechanism for avoiding damage, or an activity useful in stimulating and coordinating reproduction, or a device for saving time to spend, instead, on the immediacies of courtship. Doubtless all these notions are true some of the time, to some degree, and in some species. Yet, even allowing for evolutionary inefficiency and for the importance of minute selective advantage, these suggestions do not seem to be enough. They simply do not explain why the greatest variety of morphological details in fiddlers are used only in intermale combat.

So, the ultimate reasons for *Uca*'s trend toward sociality remain mysterious. Vast numbers of marine invertebrates, from corals upward, have lived successfully under crowded conditions with no notable development of social behavior at all. *Uca,* in contrast, has developed its wealth of social intricacies. Threatening, fighting, rubbing, and tapping one another, stridulating, drumming, building, chasing, waving, curtsying, droving—these and all their further complexities have evolved from simple beginnings traceable quite distinctly in living species. Limitations in the basic amphibious plan of fiddler existence will probably discourage much further evolution. Meanwhile all over the world their habitats diminish.

Yet right now these lively crabs are flourishing and await the further study which is their due. Our understanding is small and their achievement great. Opportunities for a practicing biologist are just about unlimited.

H. SUMMARY

As in many other animals, the characters in *Uca* that are most helpful in deciphering relationships and phylogenetic history are those connected ultimately with reproduction. In contrast more conservative structures and behavior patterns maintain the individual. The traits showing the greatest diversity are the armature of appendages and orbits, form of gonopod, and patterns of waving display. Allopatric divisions are most prevalent in the heart of the Indo-Pacific, where orogenic action subjected the fauna to temporary partitions; marginal populations, on the other hand, in this genus are conservative; intermediate are forms living along the relatively unbroken coasts of Africa and America.

Differences in waving display and gonopod shape are apparently important means through which forms living in close sympatry avoid wasted courtship time and ineffective matings. In several species either the display or the gonopod or both show changes from their expectable patterns when the range coincides in part with that of a close relation. Since in sympatric communities breeding periods are usually synchronous and habitats overlapping, seasons and niches are largely ineffective in maintaining specific barriers.

The strongest stimuli to speciation in *Uca* were probably the presence of available biotopes in America and the intermittent barriers of both the Panamanian isthmus and the Sunda Shelf. The subgenera showing the highest specializations in both structure and behavior appear to have arisen in America. The degrees of differences are described that developed during the known periods of isolation. A phylogeny is proposed in which the Indo-Pacific subgenus *Deltuca* is held to be closest to the ancestral stock, while the American subgenus *Celuca* shows the greatest number of species and extremes of specializations. The genus as a whole has evolved in three principal directions. The first of these has been toward a more terrestrial environment, through devices for avoiding desiccation and for utilizing food from the upper littoral; the second, toward sympatric sharing of habitats, is aided by miniaturization as well as by structural and behavioral differences; the third and last trend has been toward increasing complexity of social organization.

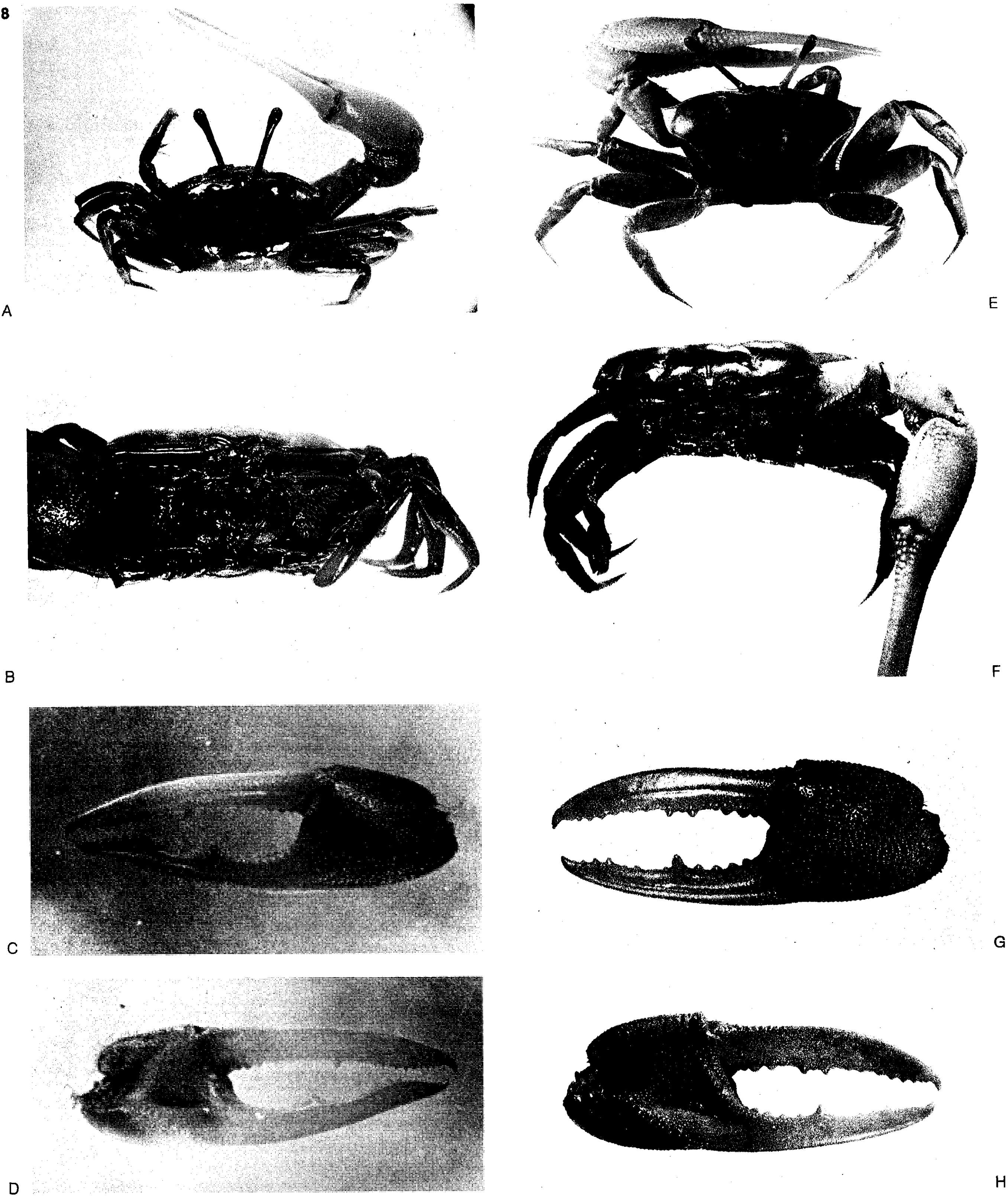
Plates

INTRODUCTION

In every plate in which four aspects of a specimen or specimens are illustrated that are members of one species or subspecies, *A* and *E* are dorsal views; *B* and *F*, anterior views; *C* and *G*, outer views of the major claw (propodus and dactyl); *D* and *H*, inner views of the major claw. For nomenclature of the parts, see Figs. 1, 2, 3, 42, 43, and 44, as well as Table 13. In plates where four aspects are not illustrated, the views are individually identified; the word "claw" always refers to the major claw.

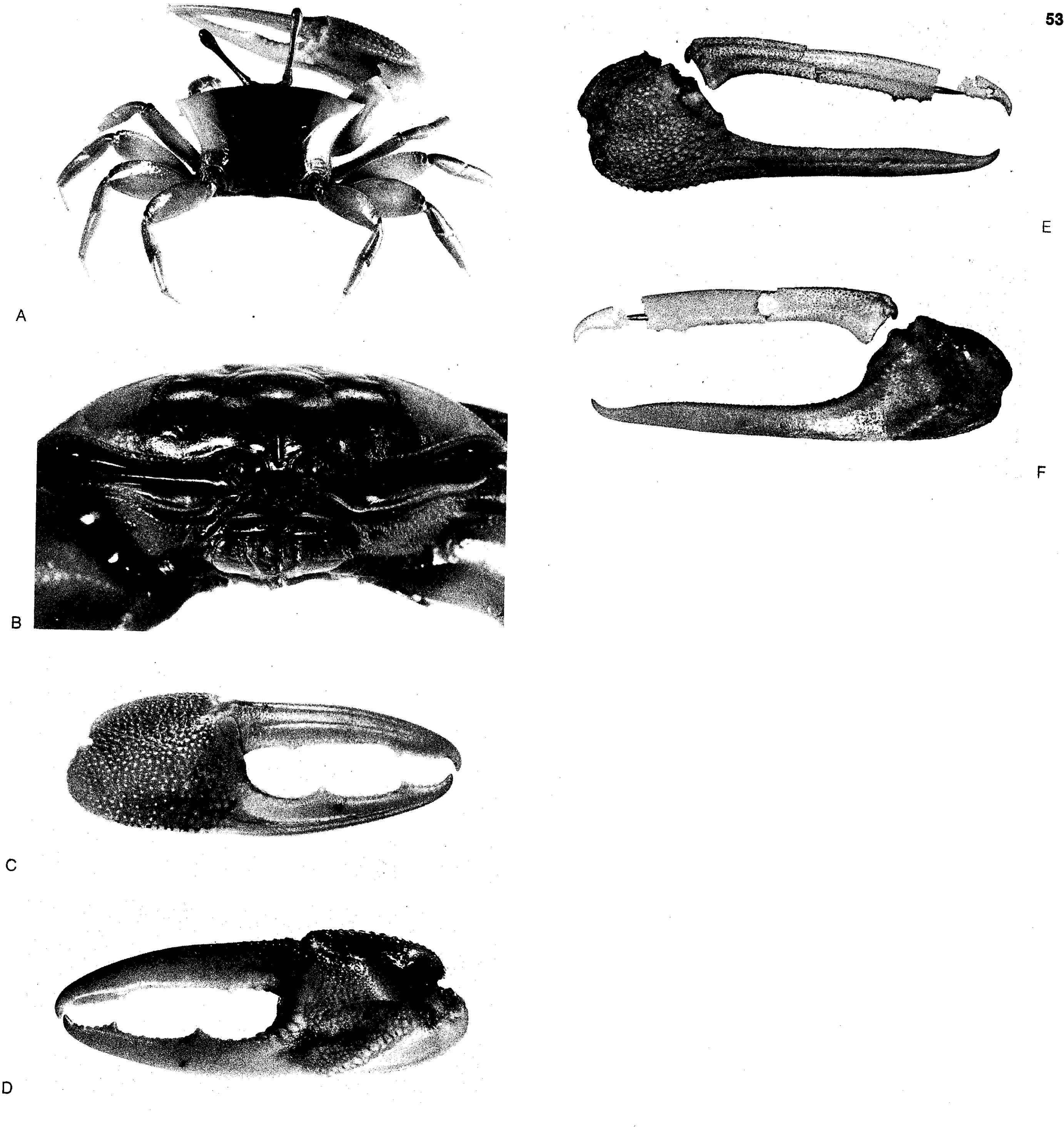
In the captions the carapace length of the specimen photographed is stated, in the belief that it will give a better idea of the size of the specimen than would the degree of magnification or the dimensions of the front or claw.

Abbreviations of institution names, given in full on p. 678, indicate the sources of photographed specimens and include catalogue numbers where these are available. All NYZS specimens are now on deposit in the USNM (see p. 591).



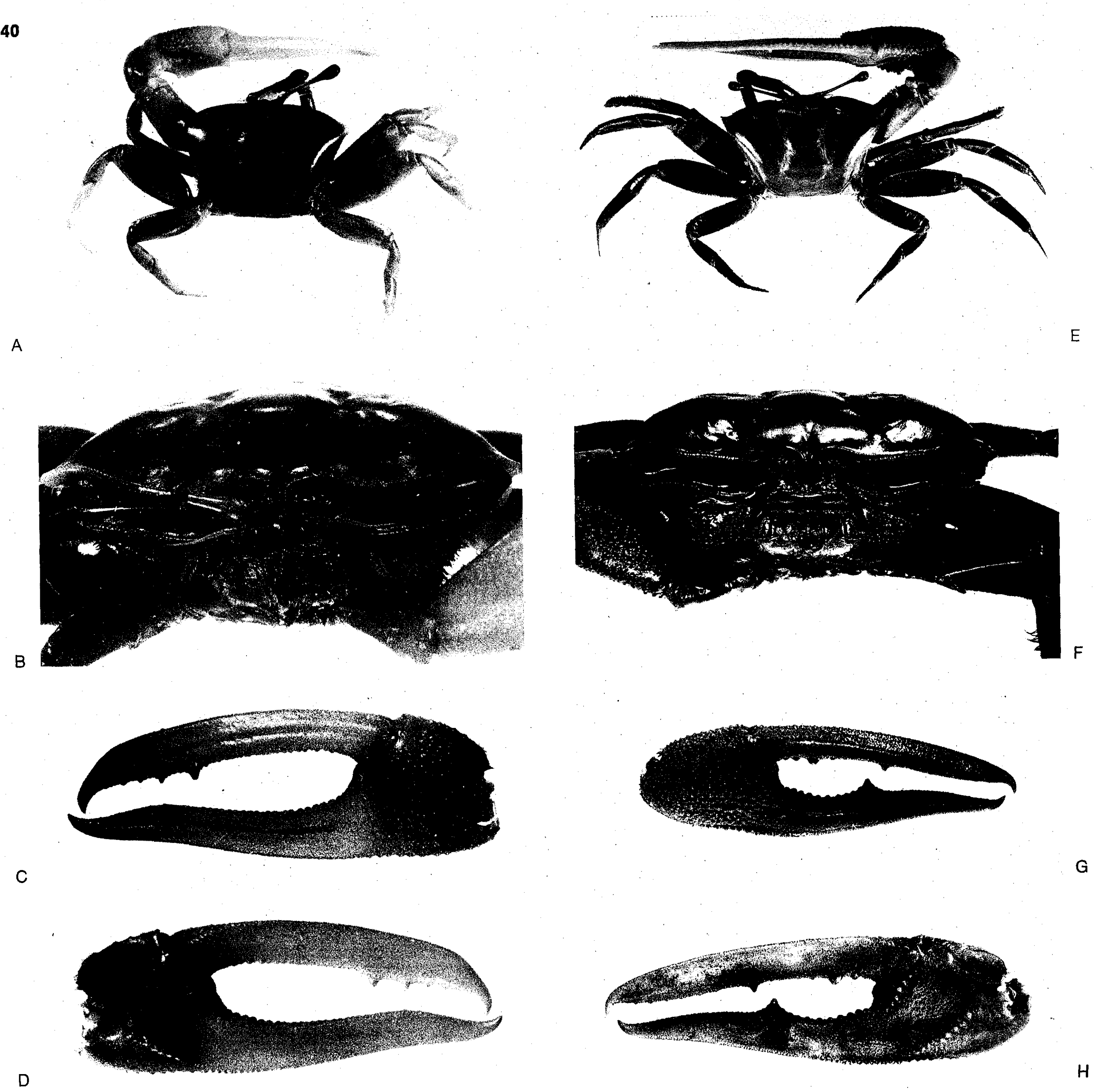
PL. 1. *A-D*. *Uca* (*Deltuca*) *acuta rhizophorae*. Sarawak: Santobong. Carapace lgth. 10 mm. NYZS. (P. 27.)

E-H. *Uca* (*Deltuca*) *acuta acuta*. China. Carapace lgth. 13 mm. USNM 57033. (P. 28.)



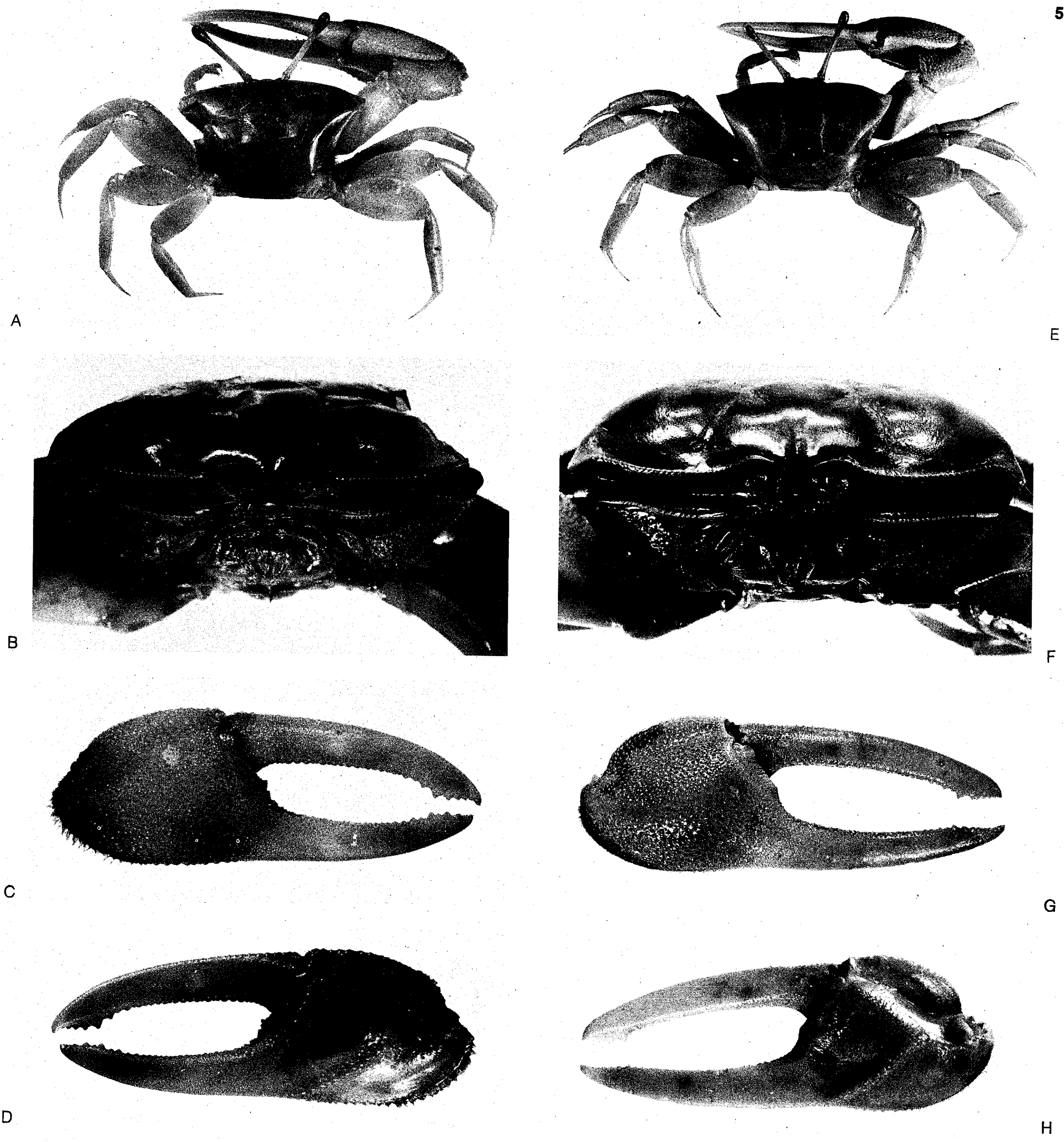
PL. 2. *A-D*. *Uca* (*Deltuca*) *rosea*. Malaya: Penang. Carapace lgth. 12 mm. NYZS. (P. 29.)

E-F. *Uca* (*Deltuca*) *dussumieri dussumieri*. Java: Semarang. Carapace lgth. 14 mm. Leptochelous individual. Paris: lectotype of *Gelasimus dussumieri*, claw. (P. 35; Figs. 8, 9.)



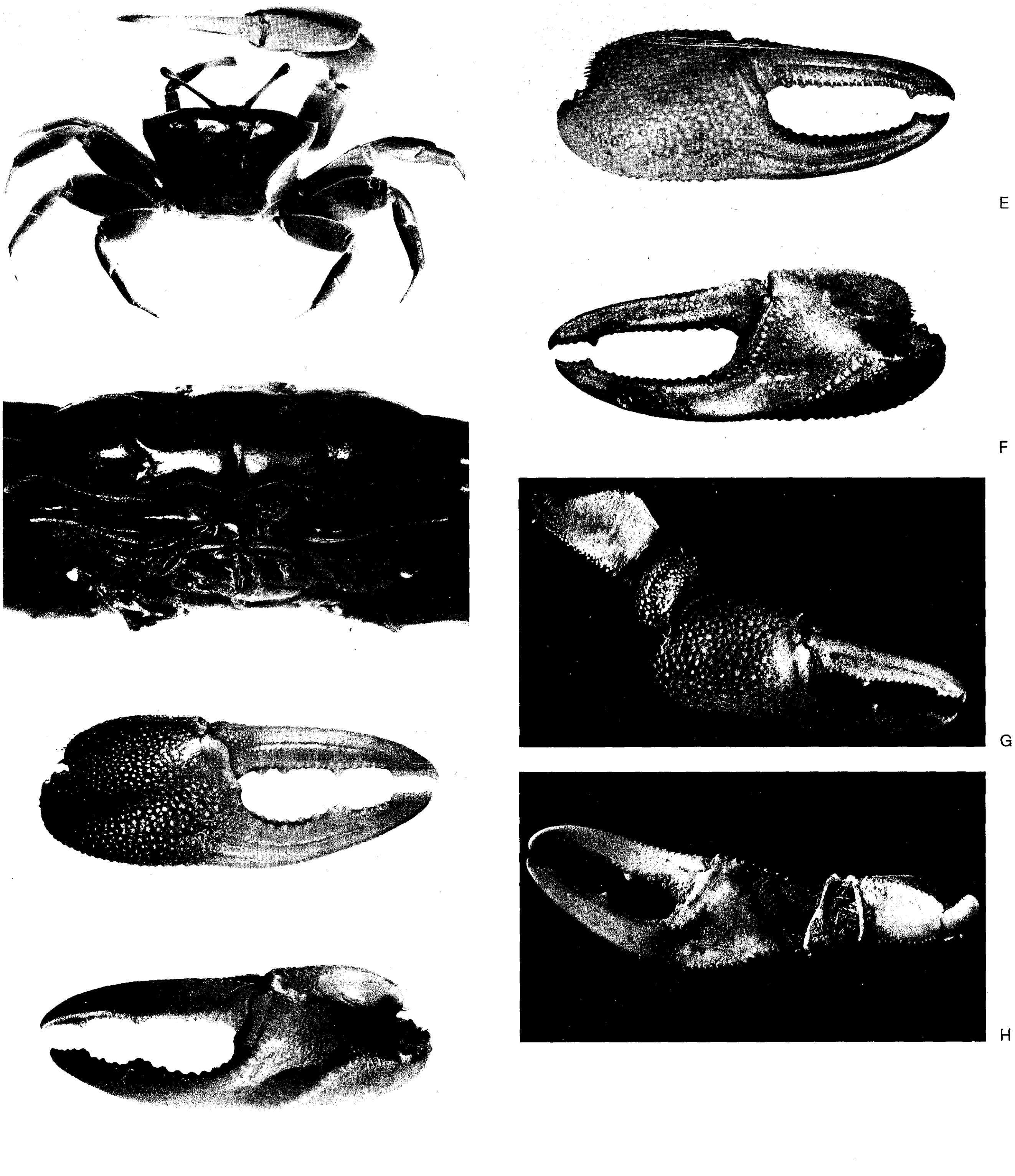
PL. 3. *A-D. Uca* (*Deltuca*) *dussumieri dussumieri.* Philippine Is.: Zamboanga. Carapace lgth. 13 mm. Leptochelous individual. NYZS. (P. 37.)

E-H. Uca (*Deltuca*) *dussumieri spinata.* Singapore. Carapace lgth. 20 mm. Brachychelous individual. NYZS. (P. 36.)



PL. 4. *A-D. Uca (Deltuca) demani australiae.* Australia: Broome. Carapace lgth. 14.5 mm. USNM 64250. (P. 41.)

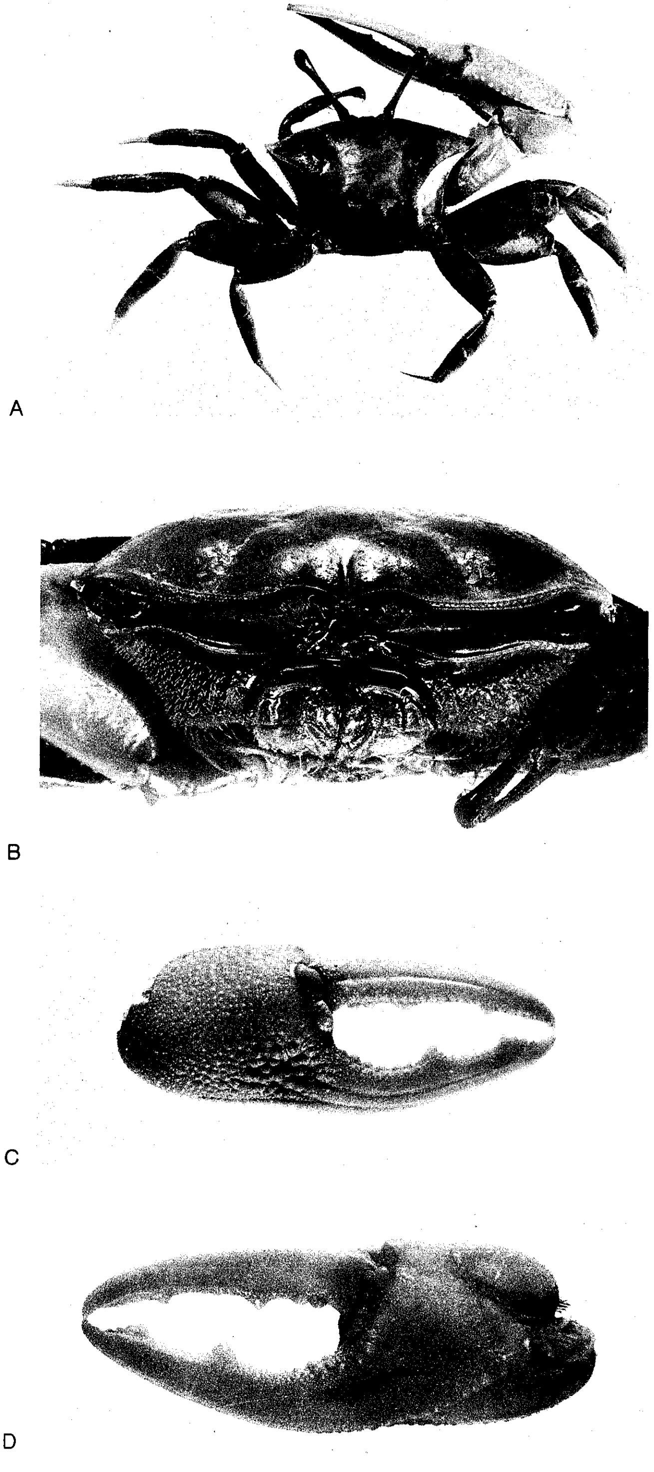
E-H. Uca (Deltuca) demani typhoni. Philippine Is.: Iloilo. Carapace lgth. 18 mm. USNM 73201. (P. 41.)

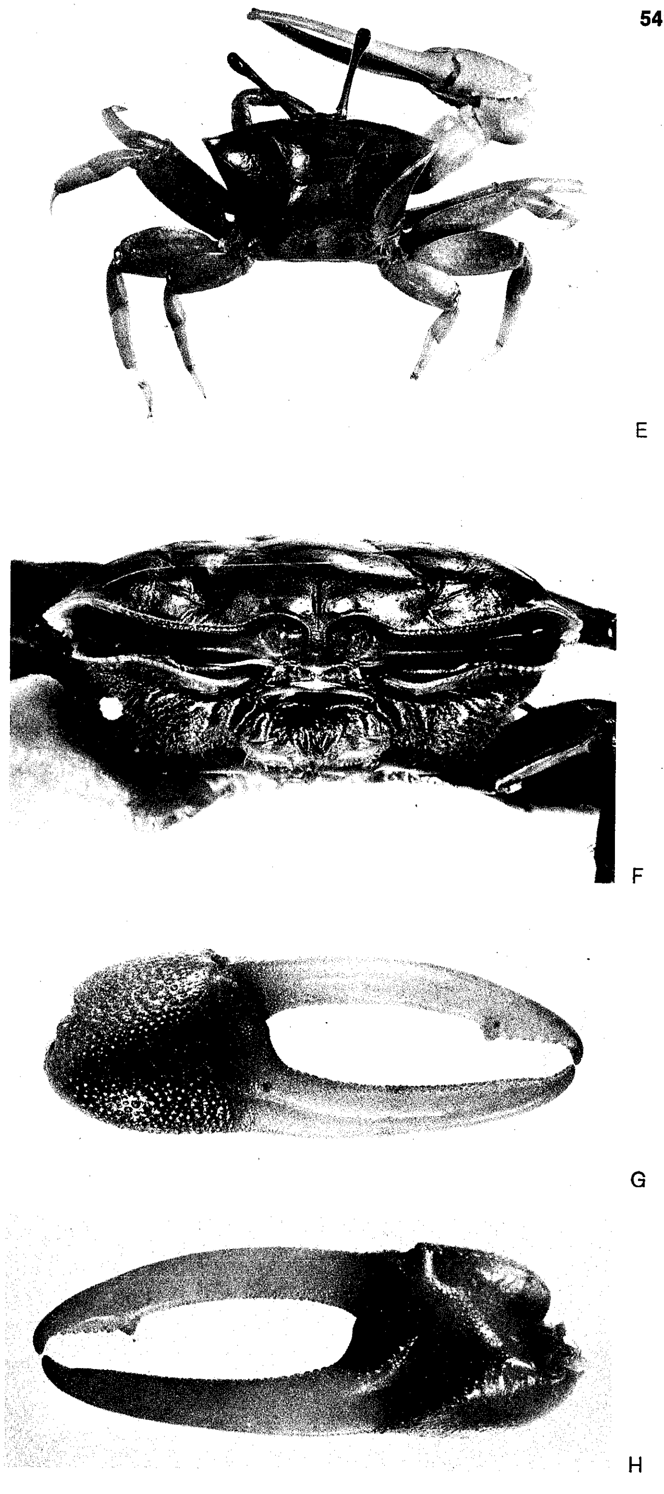


PL. 5. *A-D*. *Uca* (*Deltuca*) *arcuata*. Japan. Carapace lgth. 19 mm. USNM 17762. (P. 44.)

E-F. *Uca* (*Deltuca*) *arcuata*. China. Carapace lgth. 15 mm. Paris: from type material of *Gelasimus brevipes*; claw. (P. 47; Figs. 8, 9.)

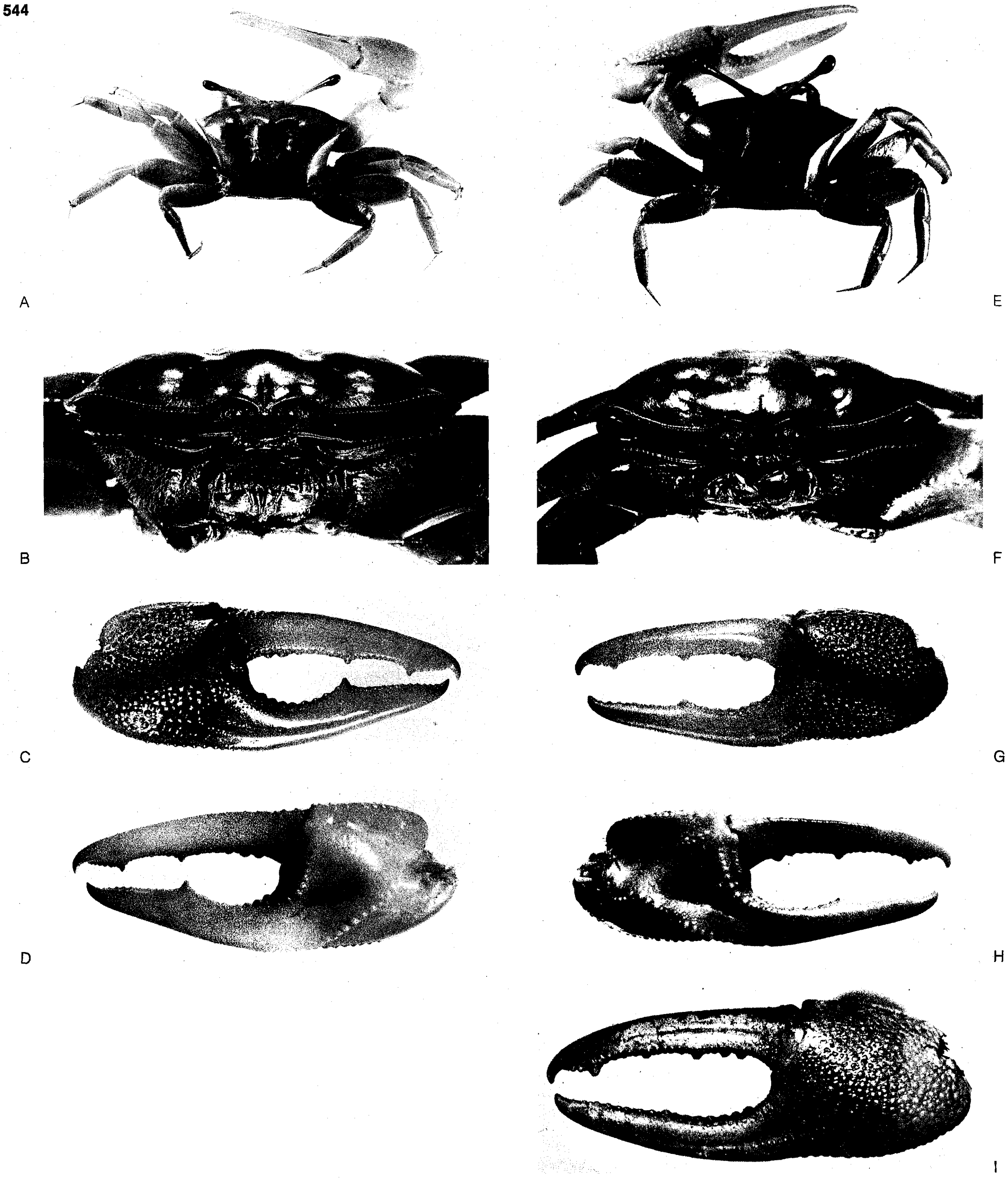
G-H. *Uca* (*Deltuca*) *forcipata*. Malaya. Carapace lgth. 10.5 mm. BM reg. no. 44.106: holotype of *Gelasimus forcipatus*; claw. (P. 51.)





PL. 6. *A-D*. *Uca* (*Deltuca*) *forcipata*. Singapore. Carapace lgth. 16 mm. NYZS. (P. 48.)

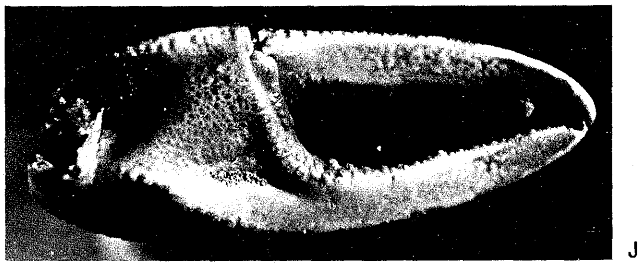
E-H. *Uca* (*Deltuca*) *coarctata coarctata*. Fiji Is. Carapace lgth. 15 mm. NYZS. (P. 55.)

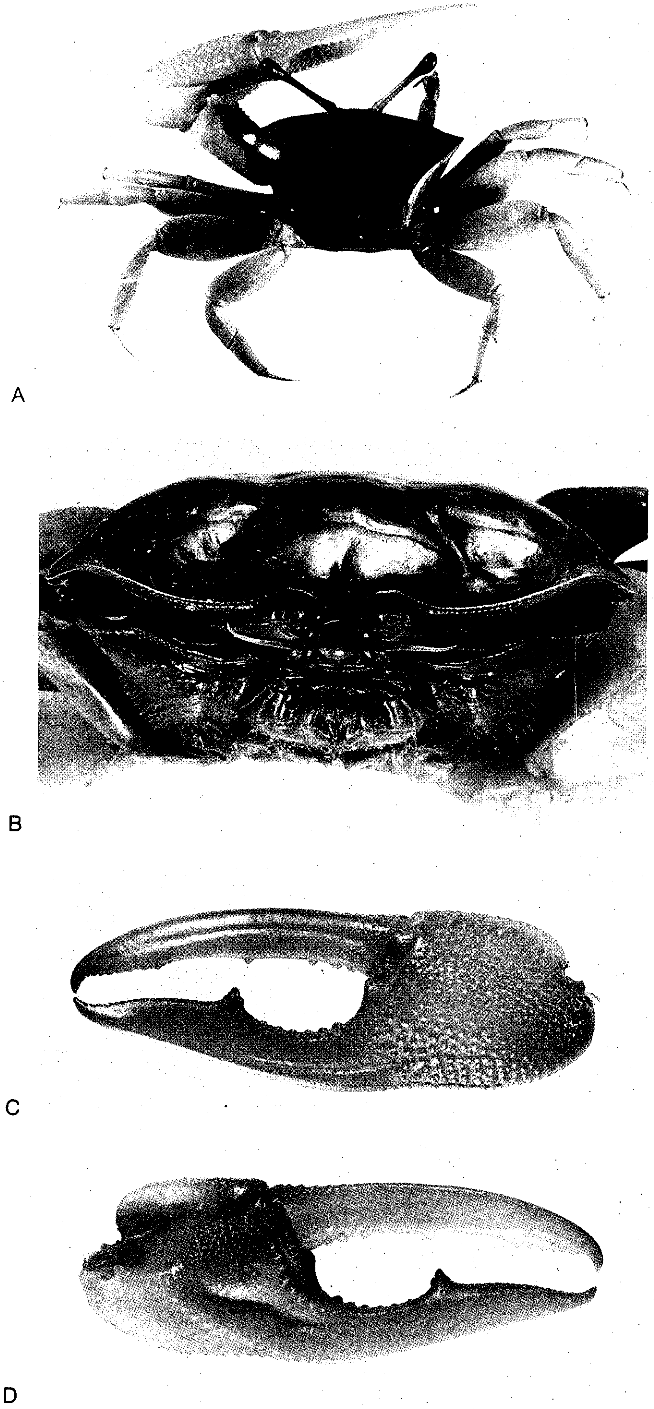


Pl. 7. *A-D. Uca* (*Deltuca*) *coarctata coarctata.* Australia: Gladstone. Carapace lgth. 16 mm. NYZS. (P. 55.)

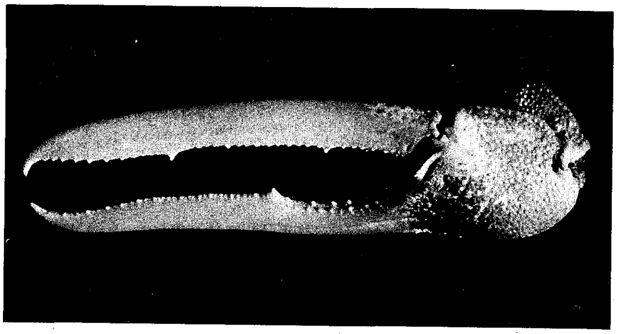
E-H. Uca (*Deltuca*) *coarctata coarctata.* Philippine Is.: near Manila. Carapace lgth. 14 mm. NYZS. (P. 55.)

I-J. Uca (*Deltuca*) *coarctata coarctata.* "Odessa." Carapace lgth. 11 mm. Paris: from type material (not lectotype) of *Gelasimus coarctatus*; claw. (P. 55.)

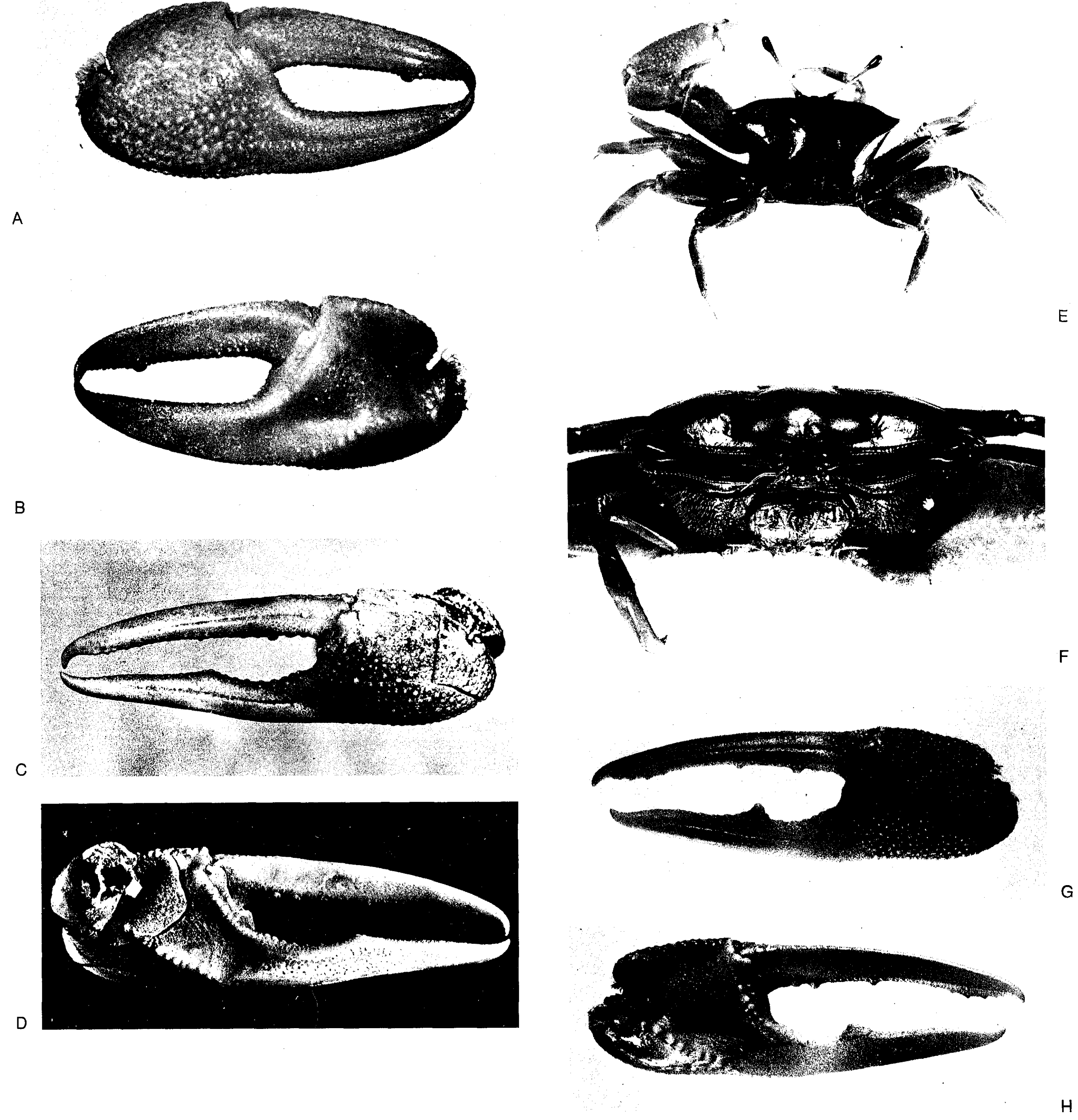




PL. 8. *A-D. Uca* (*Deltuca*) *coarctata flammula* subsp. nov. Australia: Port Darwin. Carapace lgth. 17.5 mm. NYZS. (P. 56.)



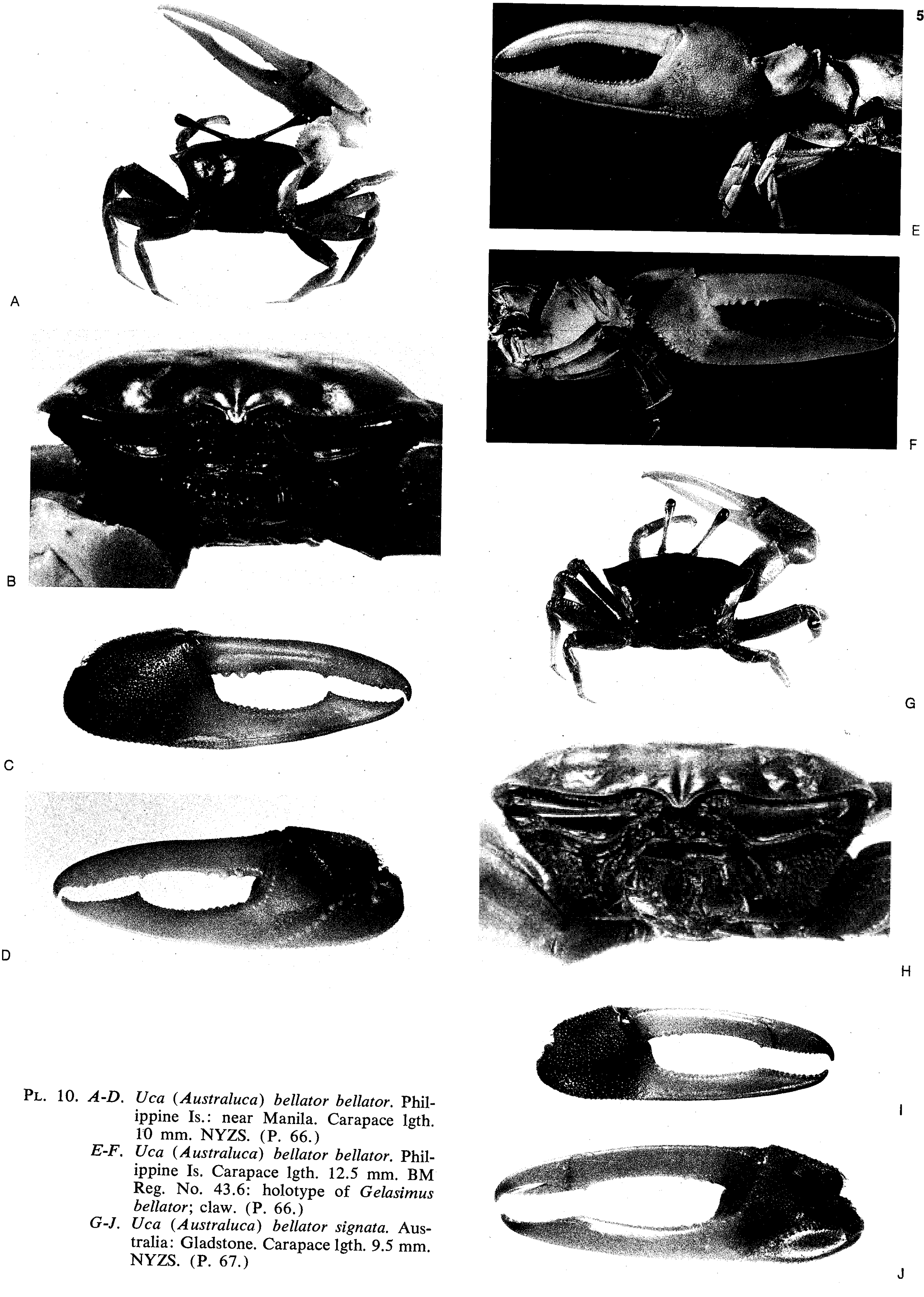
E. Uca (*Deltuca*) *coarctata flammula*. Australia: Cossack (lat. 20°40′ S., long. 117°5′ E.). Propodus lgth. 75 mm. Collection of Wm. Macnae; outer claw.



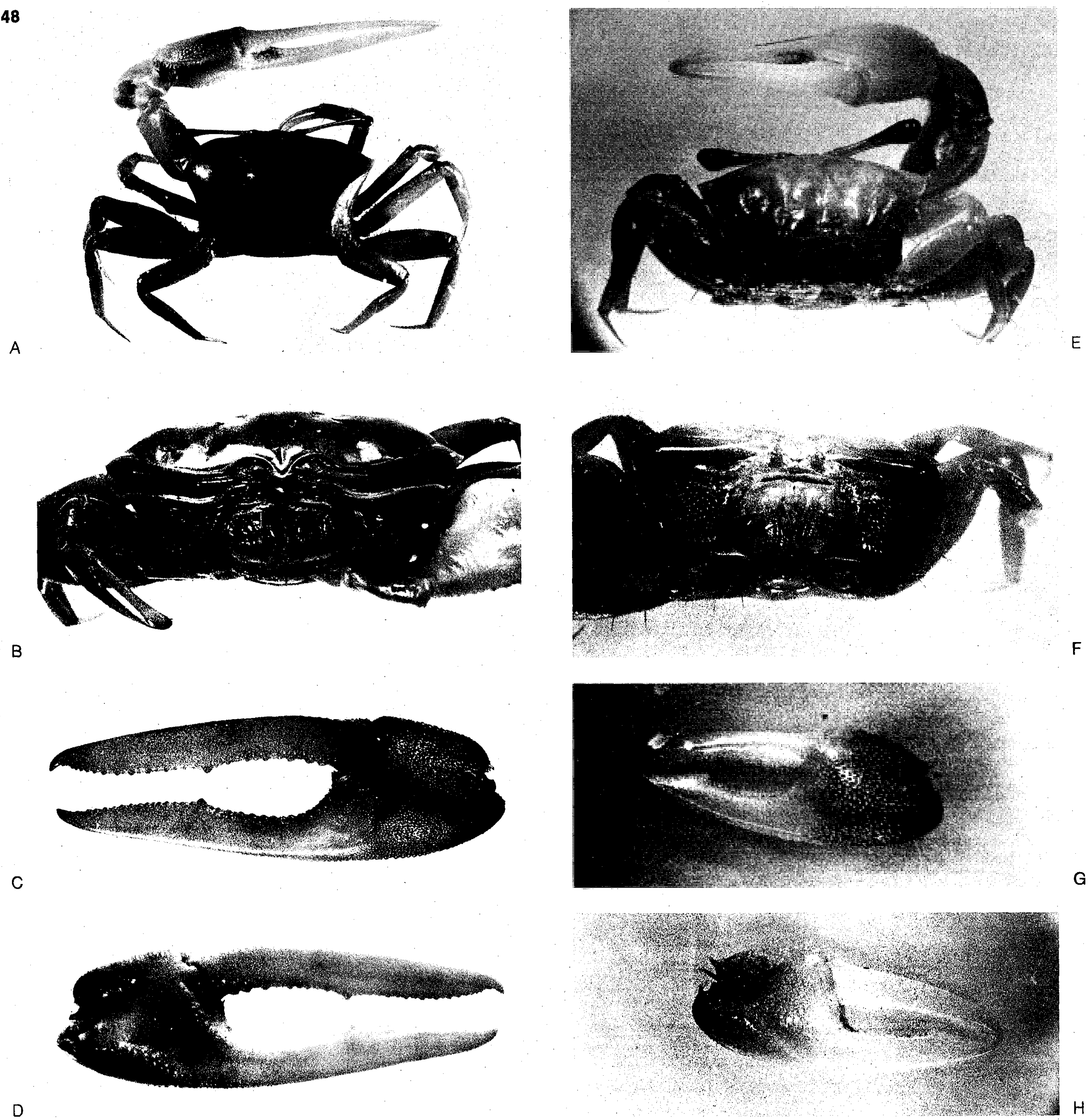
Pl. 9. *A-B*. *Uca* (*Deltuca*) *urvillei*. "Vanikoro." Carapace lgth. 11 mm. Paris: Type of *Gelasimus urvillei*; claw. (P. 60; Figs. 8, 9.)

C-D. *Uca* (*Deltuca*) *urvillei*. India: Malabar Coast. Carapace lgth. 17 mm. Paris: from type material of *Gelasimus dussumieri*. (P. 60; Figs. 8, 9.)

E-H. *Uca* (*Deltuca*) *urvillei*. Tanzania: Pemba I. Carapace lgth. 18.5 mm. NYZS. (P. 58.)

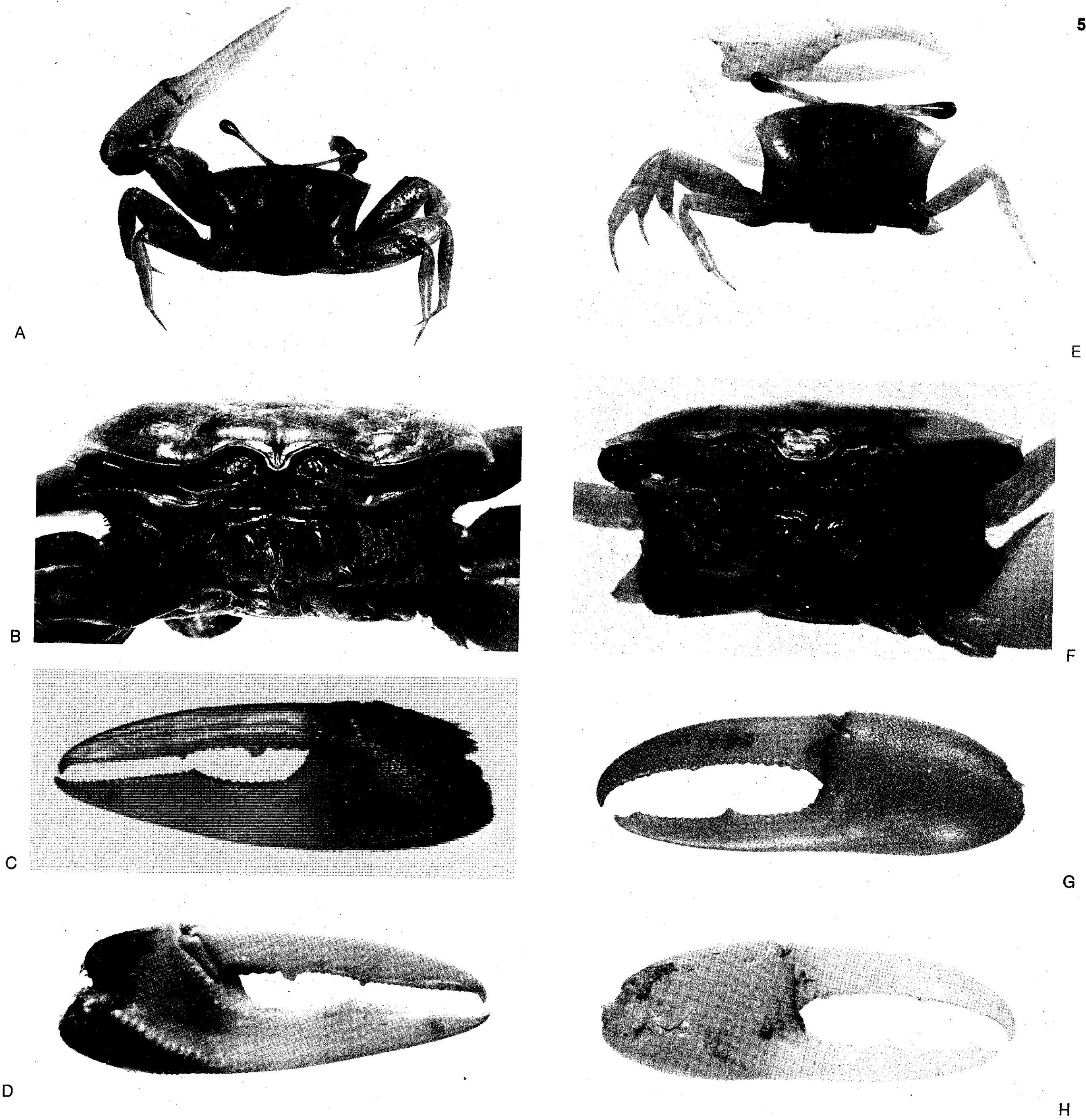


Pl. 10. *A-D*. *Uca* (*Australuca*) *bellator bellator*. Philippine Is.: near Manila. Carapace lgth. 10 mm. NYZS. (P. 66.)
E-F. *Uca* (*Australuca*) *bellator bellator*. Philippine Is. Carapace lgth. 12.5 mm. BM Reg. No. 43.6: holotype of *Gelasimus bellator*; claw. (P. 66.)
G-J. *Uca* (*Australuca*) *bellator signata*. Australia: Gladstone. Carapace lgth. 9.5 mm. NYZS. (P. 67.)



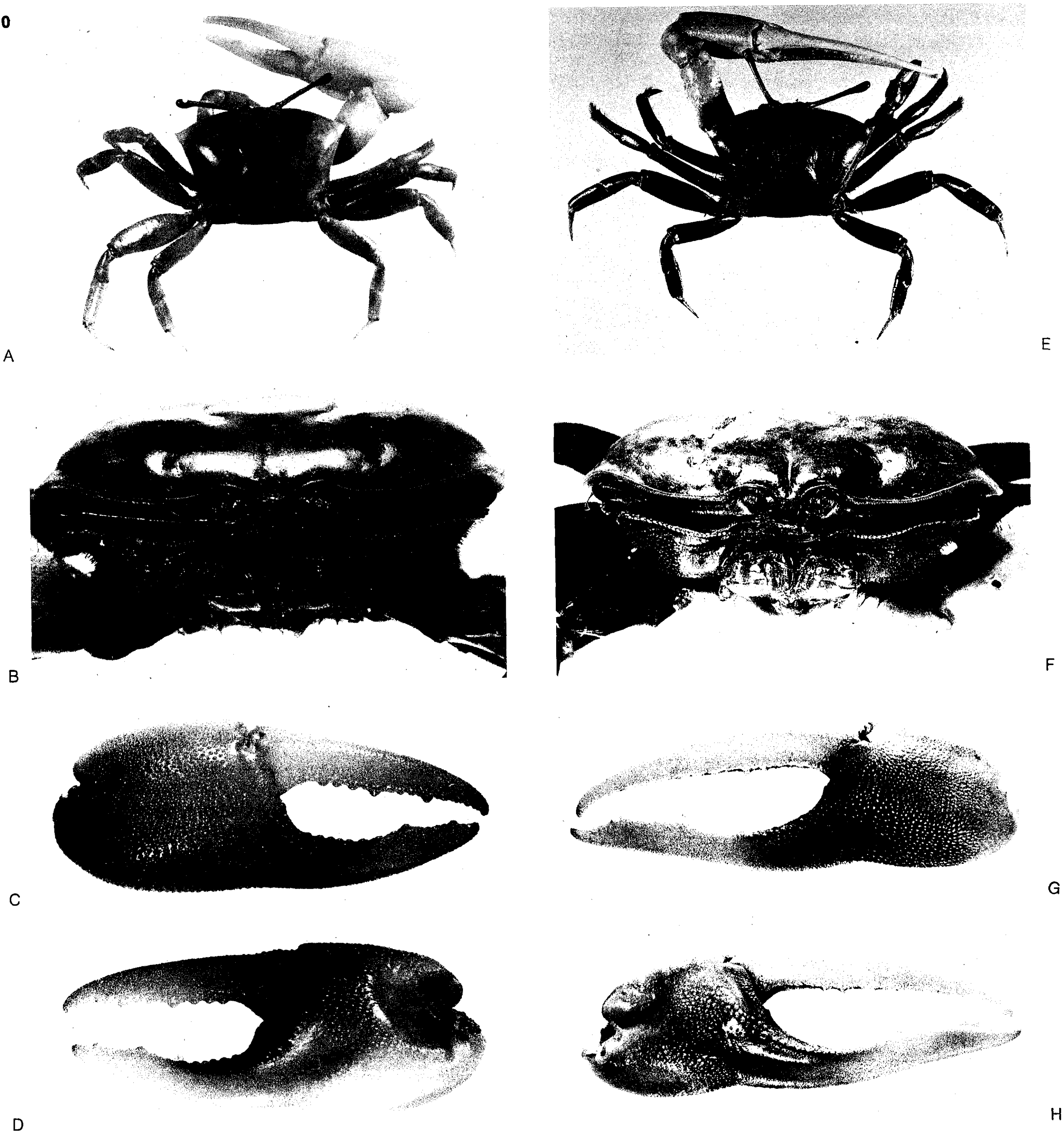
PL. 11. *A-D. Uca* (*Australuca*) *bellator longidigita.* Australia: Brisbane. Carapace lgth. 10.5 mm. NYZS. (P. 68.)

E-H. Uca (*Australuca*) *bellator minima* subsp. nov. Australia: Port Darwin. Carapace lgth. 5 mm. NYZS. (P. 68.)



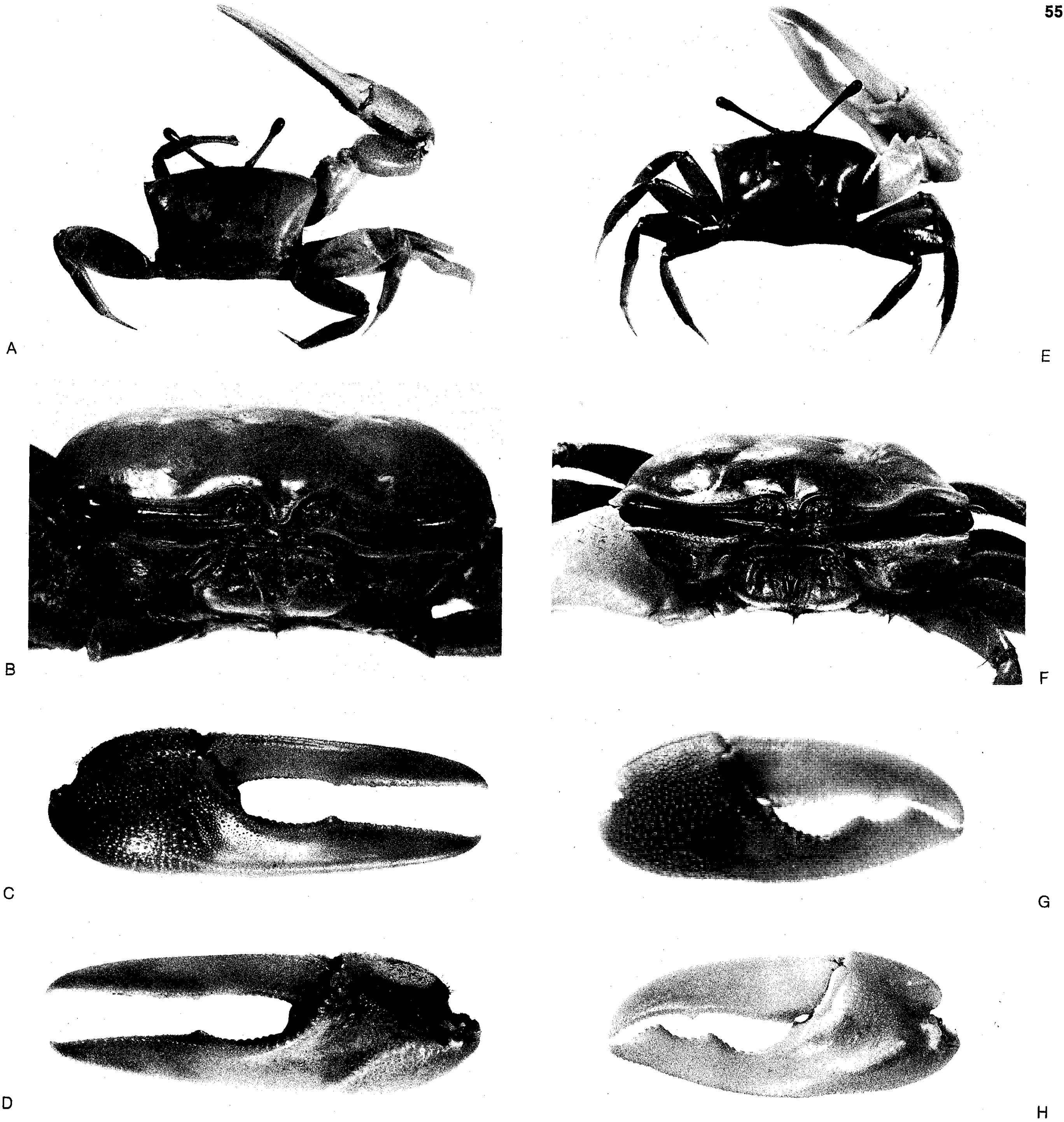
PL. 12. *A-D*. *Uca* (*Australuca*) *seismella* sp. nov. Australia: Port Darwin. Carapace lgth. 7 mm. NYZS. (P. 70.)

E-H. *Uca* (*Australuca*) *polita* sp. nov. Australia: Gladstone. Carapace lgth. 9.5 mm. NYZS. (P. 72.)



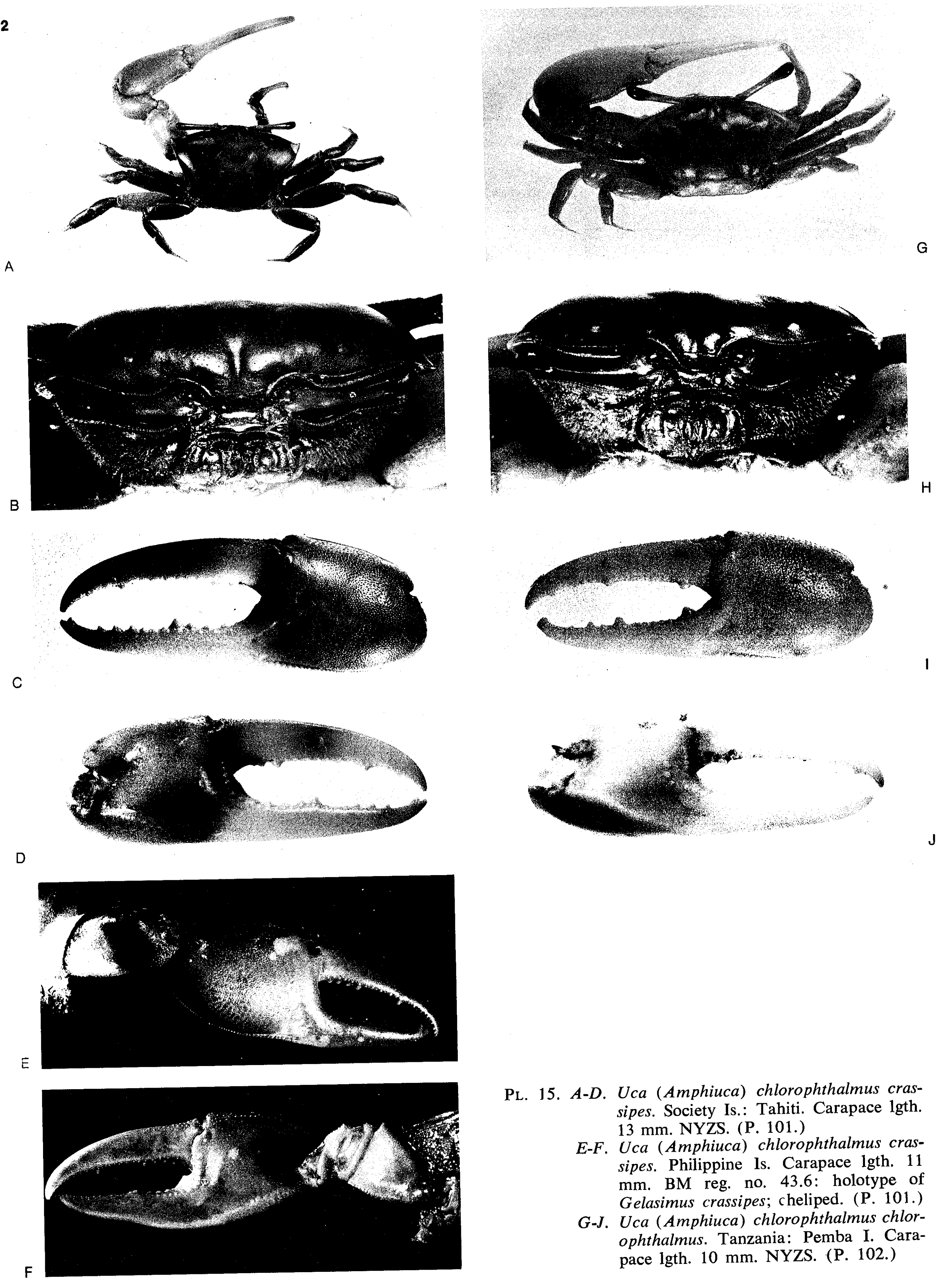
Pl. 13. *A-D. Uca (Thalassuca) tetragonon.* Ethiopia: Massawa. Carapace lgth. 16 mm. NYZS. (P. 77.)

E-H. Uca (Thalassuca) tetragonon. Society Is.: Tahiti. Carapace lgth. 22 mm. NYZS. (P. 77.)



PL. 14. *A-D*. *Uca* (*Thalassuca*) *formosensis*. Taiwan: Taihoku. Carapace lgth. 15 mm. USNM 55386. (P. 83.)

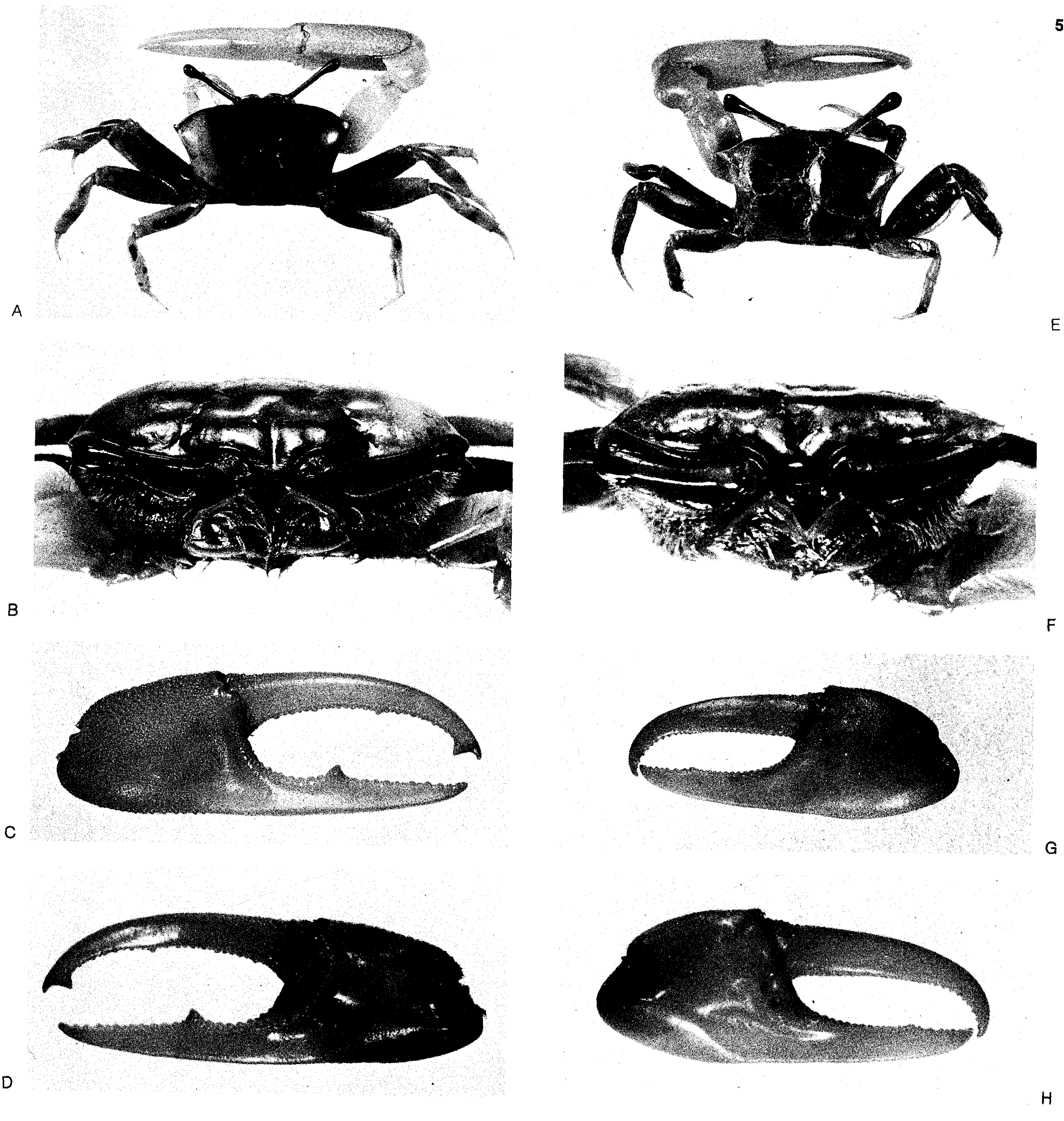
E-H. *Uca* (*Thalassuca*) *vocans vocans*. Philippine Is.: Madaum. Carapace lgth. 12.5 mm. (P. 92.)



Pl. 15. *A-D. Uca* (*Amphiuca*) *chlorophthalmus crassipes.* Society Is.: Tahiti. Carapace lgth. 13 mm. NYZS. (P. 101.)

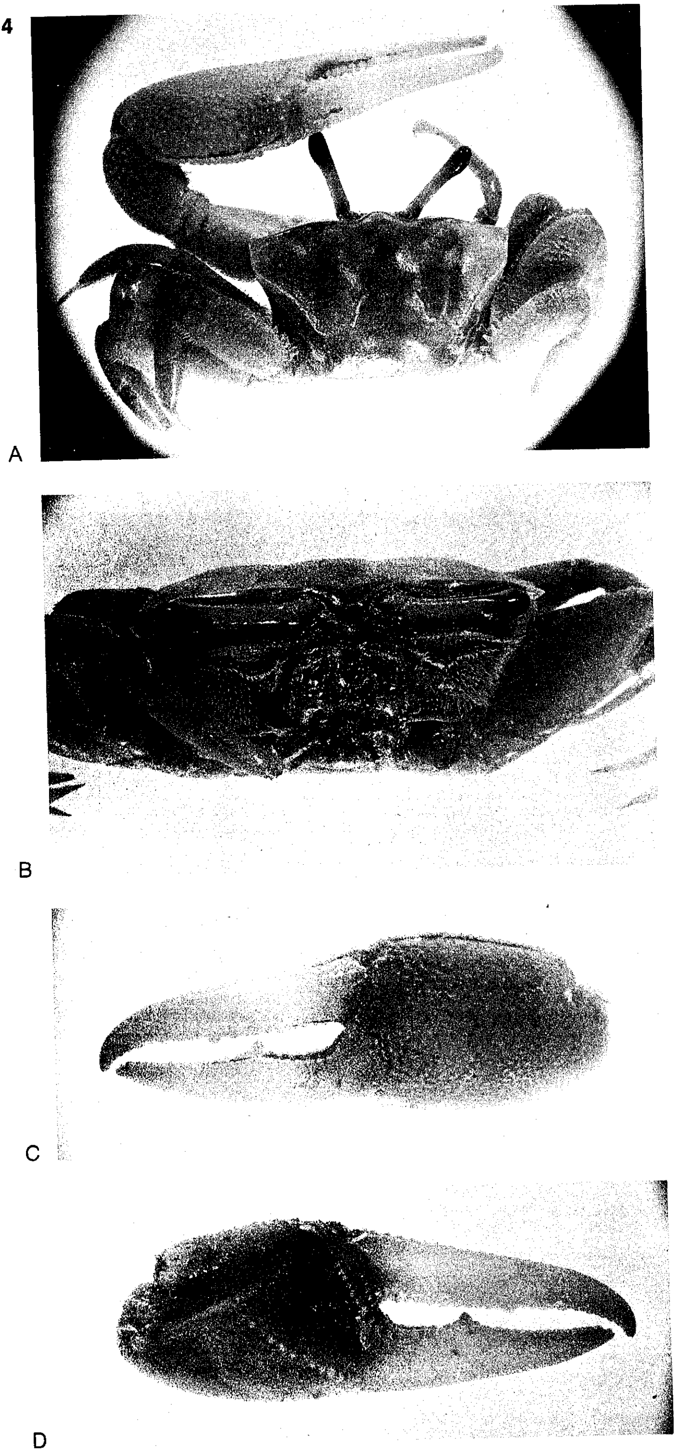
E-F. Uca (*Amphiuca*) *chlorophthalmus crassipes.* Philippine Is. Carapace lgth. 11 mm. BM reg. no. 43.6: holotype of *Gelasimus crassipes*; cheliped. (P. 101.)

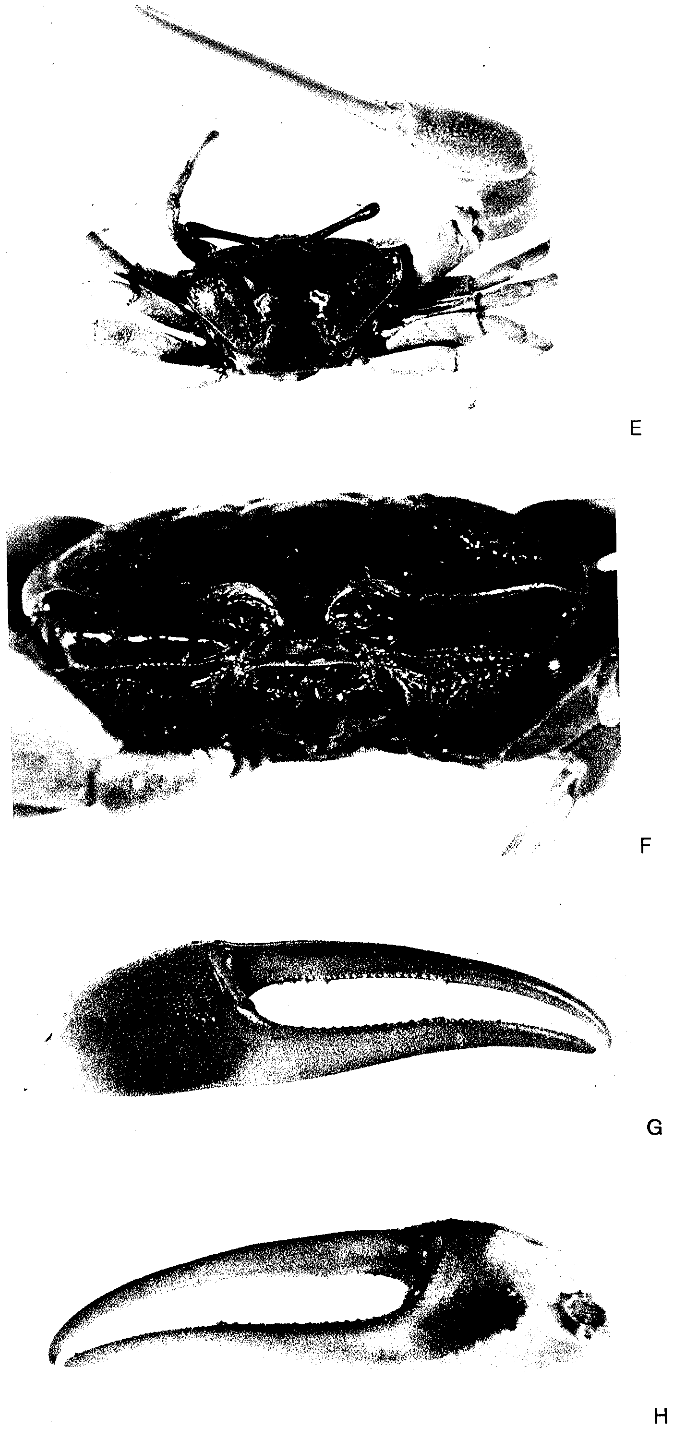
G-J. Uca (*Amphiuca*) *chlorophthalmus chlorophthalmus.* Tanzania: Pemba I. Carapace lgth. 10 mm. NYZS. (P. 102.)



Pl. 16. *A-D. Uca* (*Amphiuca*) *inversa inversa.* Tanzania: Zanzibar. Carapace lgth. 11 mm. NYZS. (P. 107.)

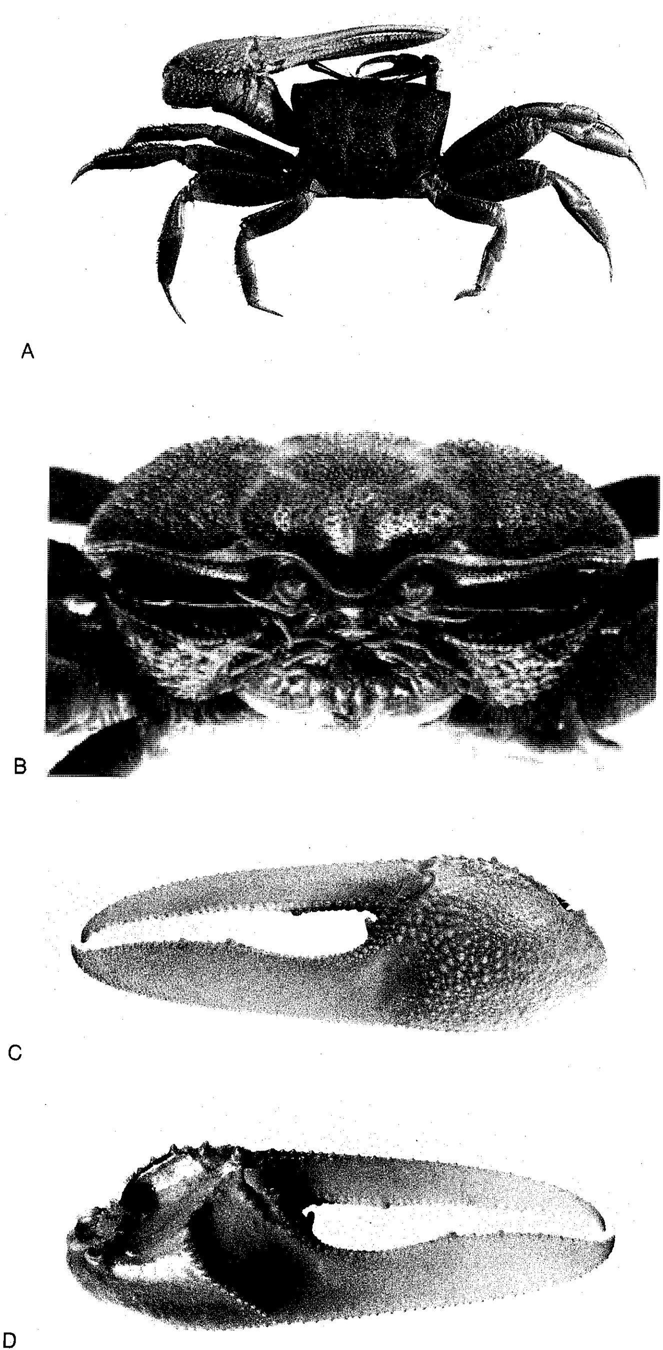
E-H. Uca (*Amphiuca*) *inversa sindensis.* Pakistan: Karachi. Carapace lgth. 7 mm. NYZS. (P. 108.)

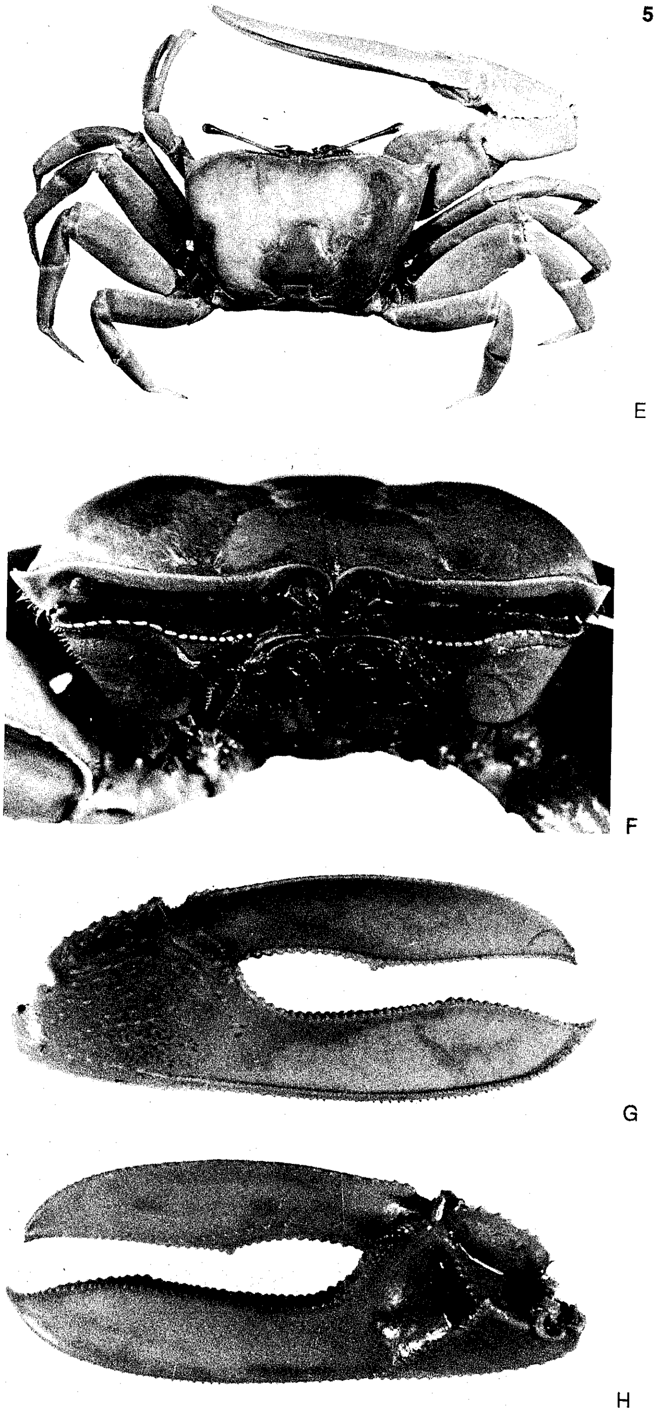




PL. 17. *A-D. Uca* (*Boboruca*) *thayeri umbratila.* Eastern Pacific: Costa Rica (Golfito). Carapace lgth. 16 mm. NYZS. (P. 113.)

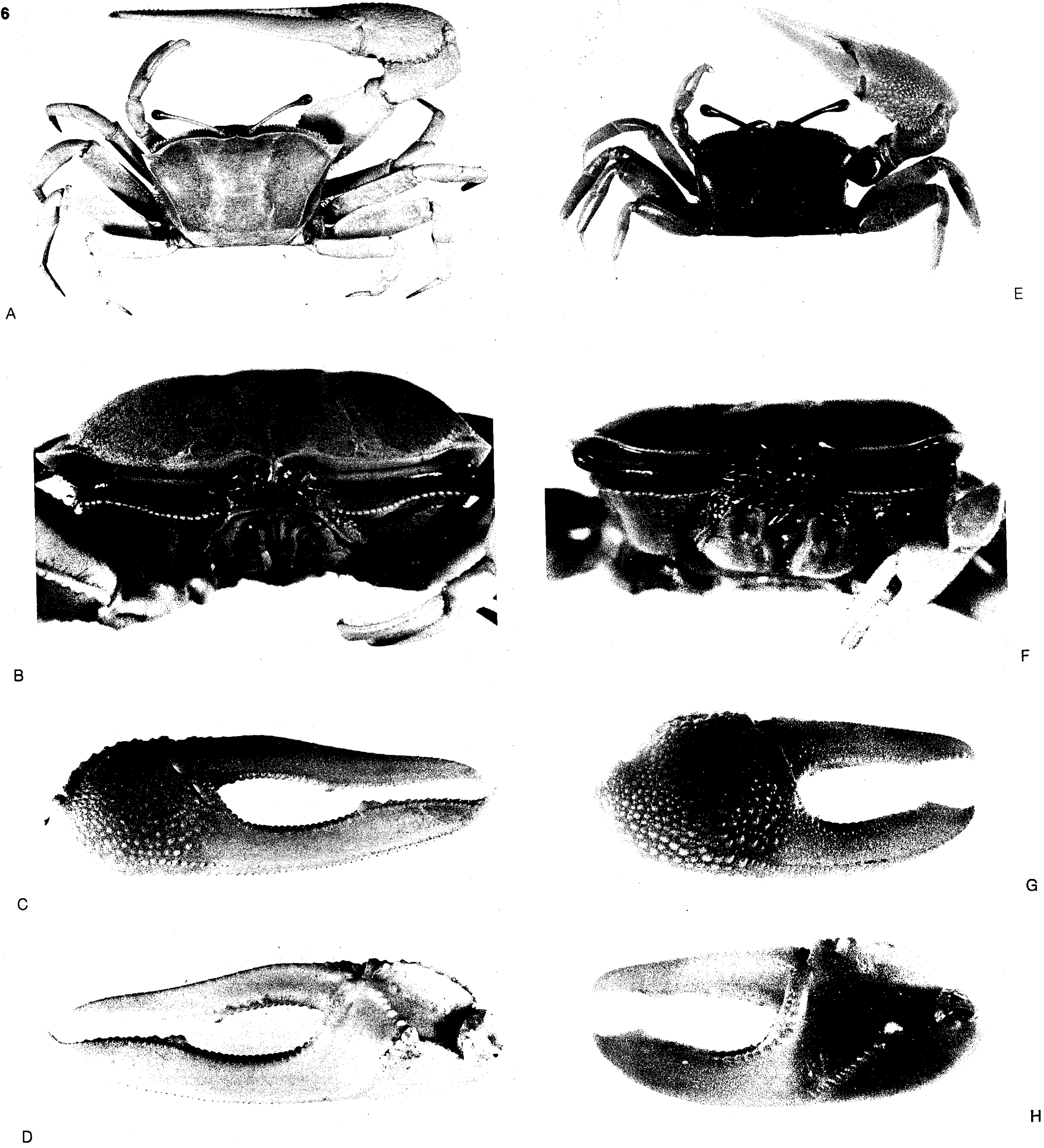
E-H. Uca (*Boboruca*) *thayeri thayeri.* West Indies: Trinidad. Carapace lgth. 17.5 mm. NYZS. (P. 114.)





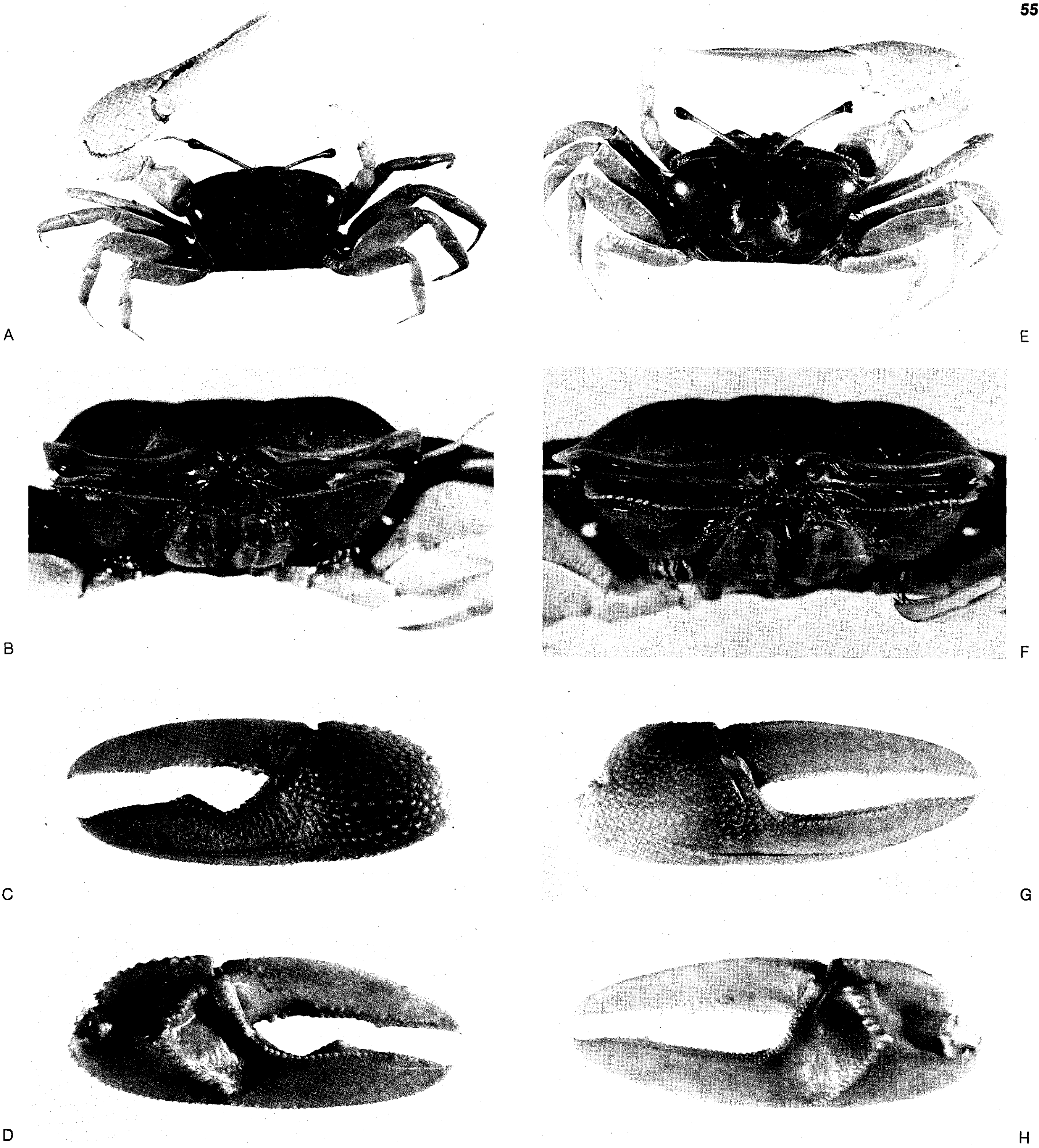
PL. 18. *A-D. Uca* (*Afruca*) *tangeri.* Angola: Luanda. Carapace lgth. 25 mm. NYZS. (P. 118.)

E-H. Uca (*Uca*) *princeps monilifera.* Mexico, in Gulf of California: San Felipe. Carapace lgth. 29.5 mm. USNM 67735. (P. 131.)



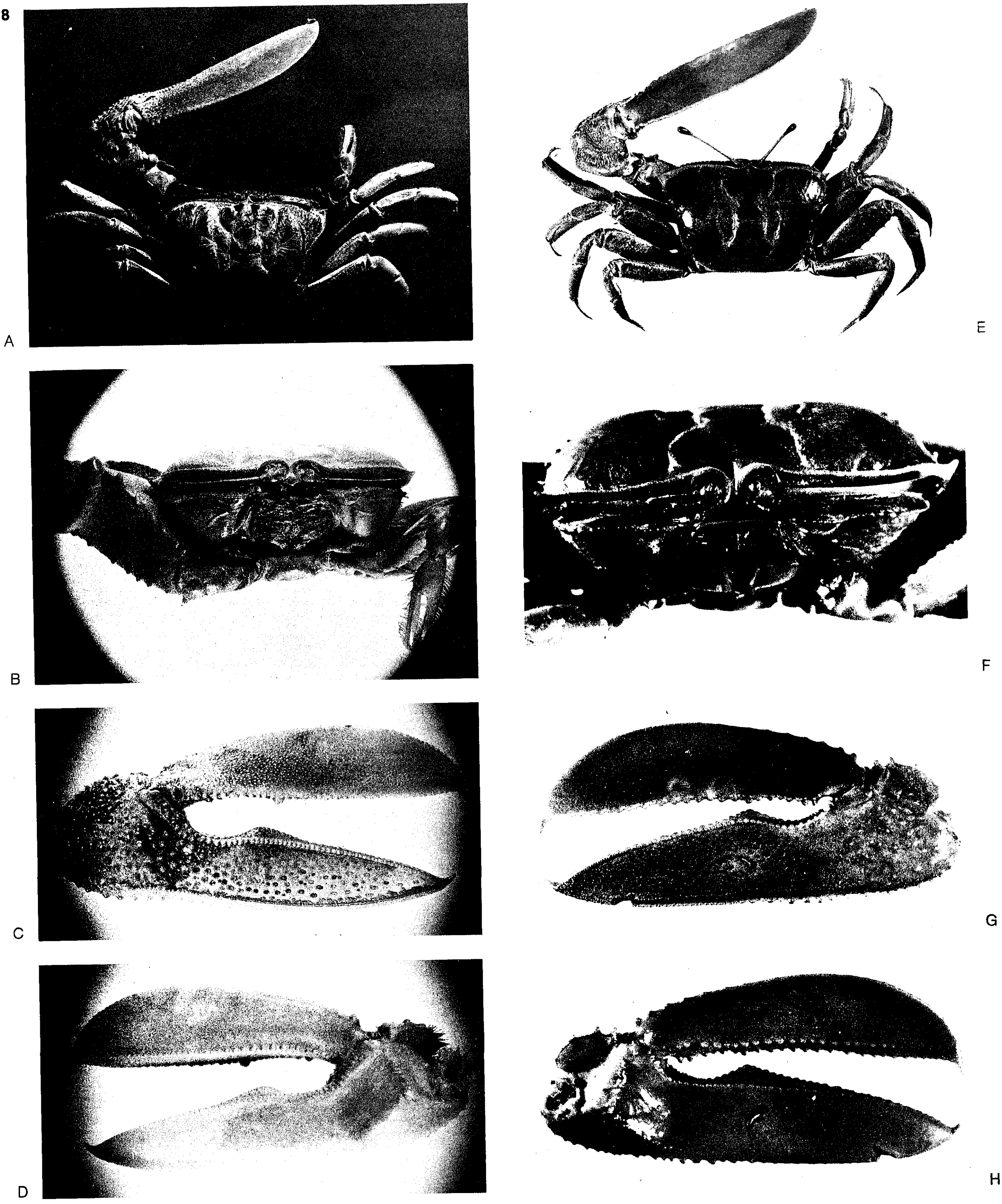
Pl. 19. *A-D. Uca (Uca) princeps princeps.* Eastern Pacific: Costa Rica (Golfito). Carapace lgth. 23 mm. NYZS. (P. 131.)

E-H. Uca (Uca) heteropleura. Eastern Pacific: Panama (Panama City). Carapace lgth. 12 mm. NYZS. (P. 133.)



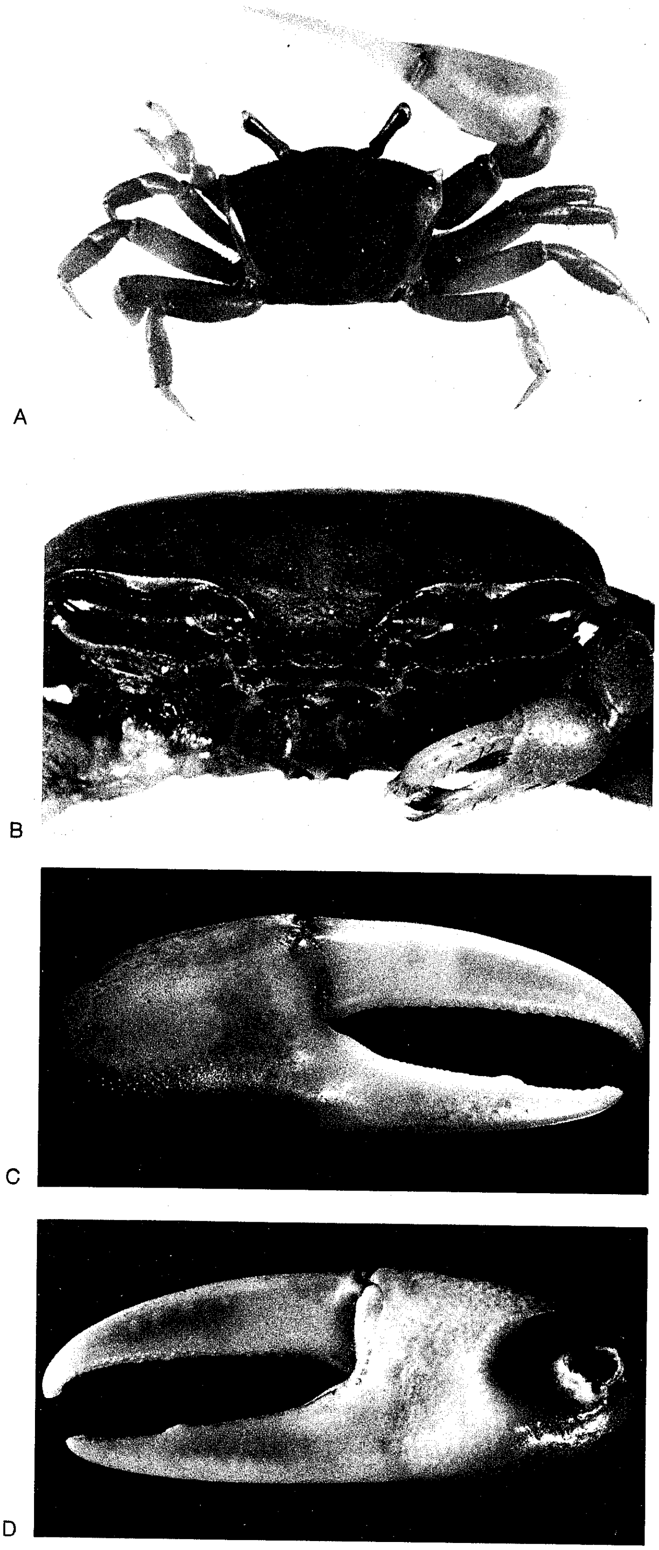
Pl. 20. *A-D. Uca* (*Uca*) *stylifera.* Eastern Pacific: Nicaragua (Corinto). Carapace lgth. 18 mm. NYZS. (P. 140.)

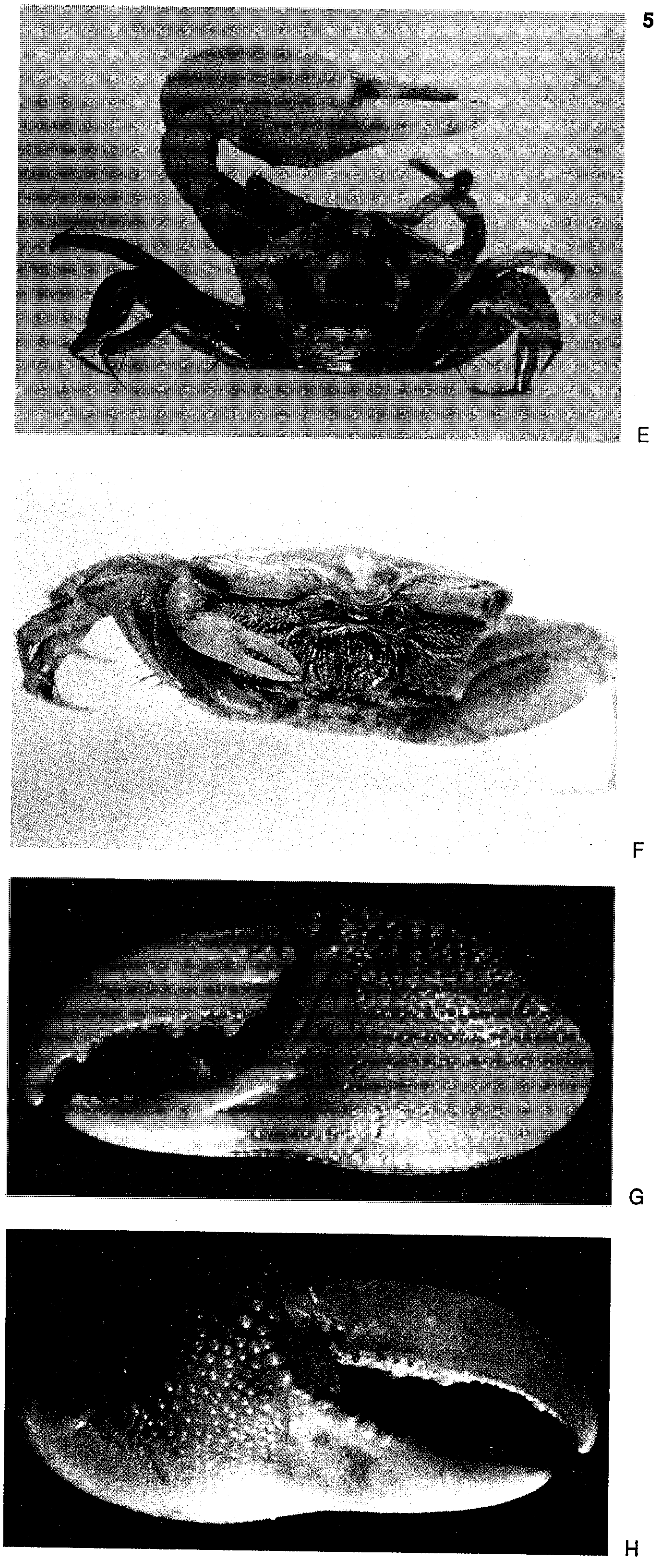
E-H. Uca (*Uca*) *major.* Venezuela: Turiamo. Carapace lgth. 14 mm. NYZS. (P. 136.)



Pl. 21. *A-D*. *Uca* (*Uca*) *maracoani maracoani*. Guyana: Georgetown. Carapace lgth. 25 mm. NYZS. (P. 147.)

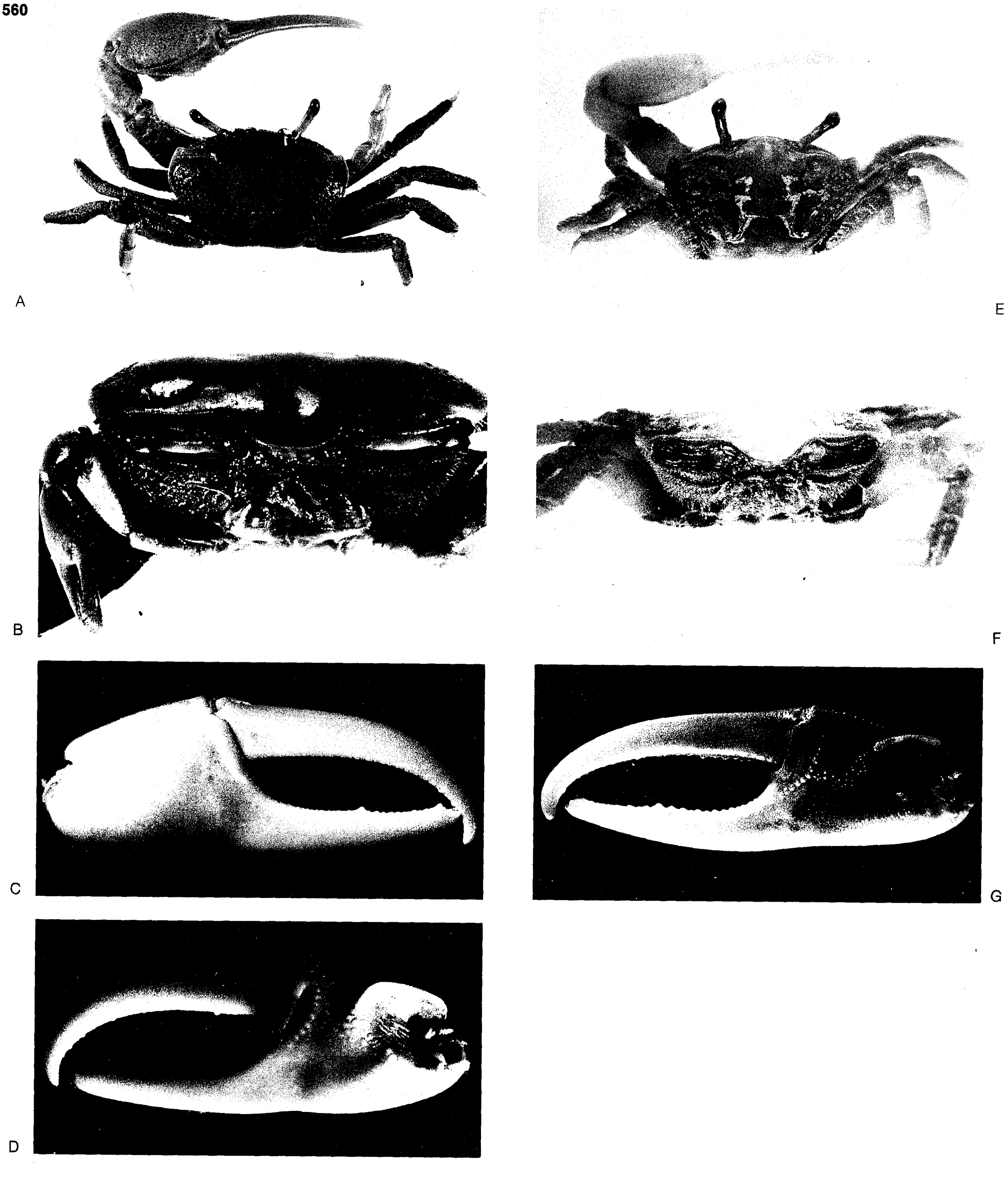
E-H. *Uca* (*Uca*) *ornata*. Eastern Pacific: Panama (Panama City). Carapace lgth. 29 mm. NYZS. (P. 150.)





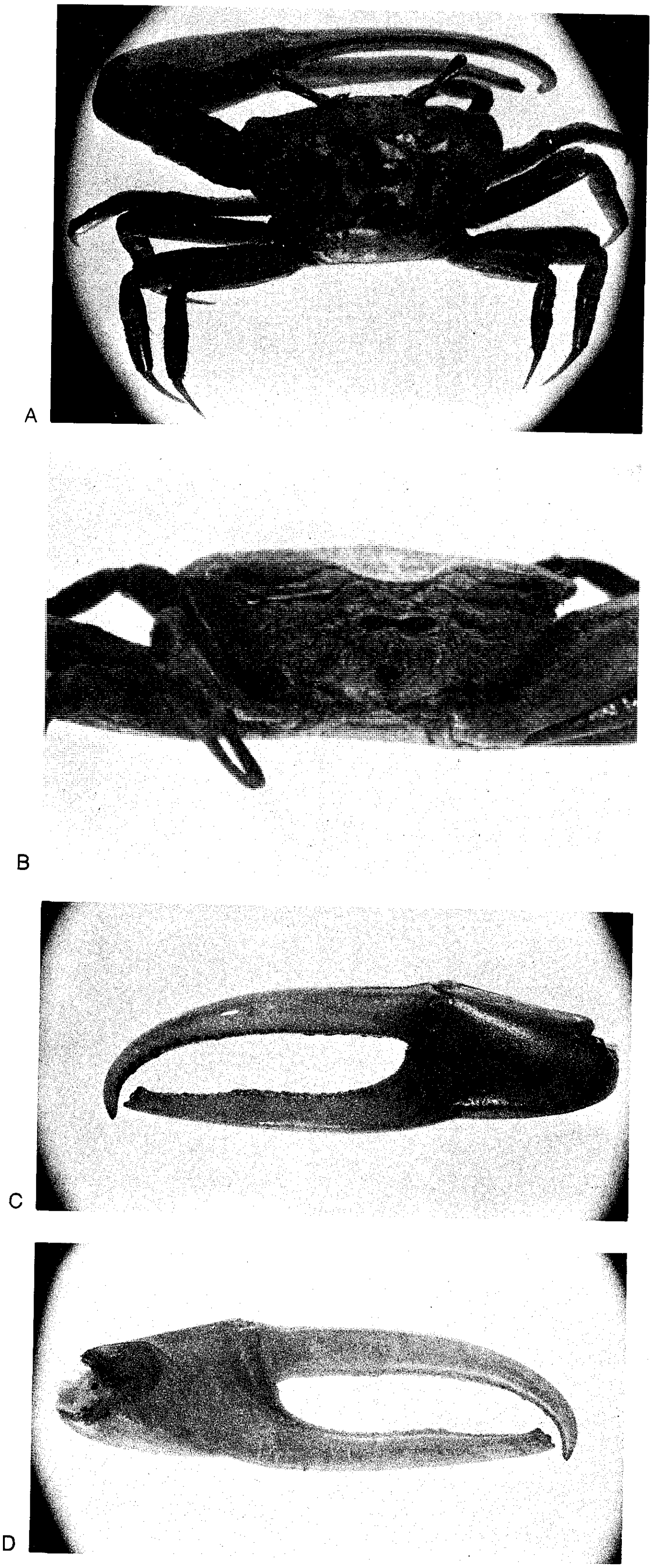
Pl. 22. *A-D*. *Uca* (*Minuca*) *panamensis*. Eastern Pacific: Colombia (Humboldt Bay). Carapace lgth. 12 mm. AMNH 7605. (P. 158.)

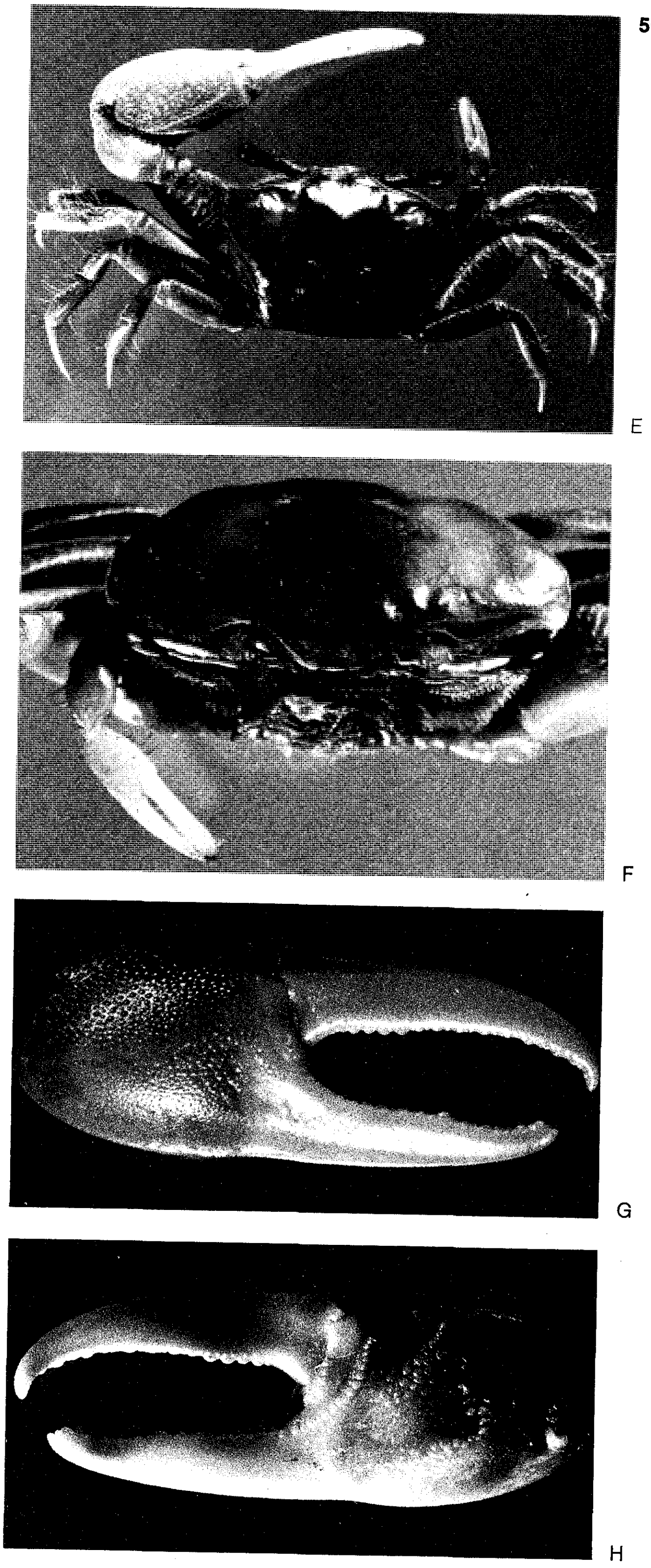
E-H. *Uca* (*Minuca*) *pygmaea*. Eastern Pacific: Colombia (Buenaventura). Carapace lgth. 6 mm. NYZS. (P. 161.)



PL. 23. *A-D. Uca (Minuca) vocator ecuadoriensis.* Eastern Pacific: Ecuador (Guayaquil). Carapace lgth. 13.5 mm. NYZS. (P. 166.)

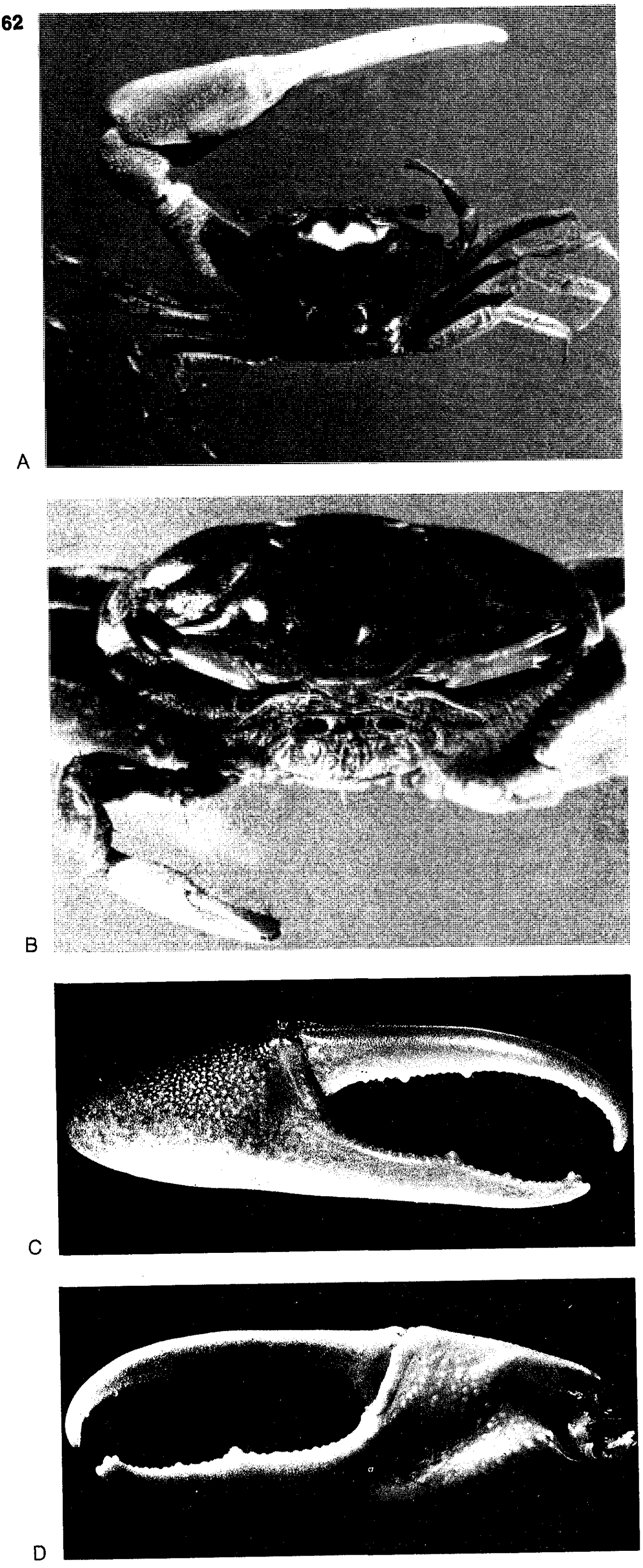
E-G. Uca (Minuca) vocator vocator. Venezuela: Maracaibo. Carapace lgth. 14.5 mm. *G* = inner side of claw. NYZS. (P. 166.)



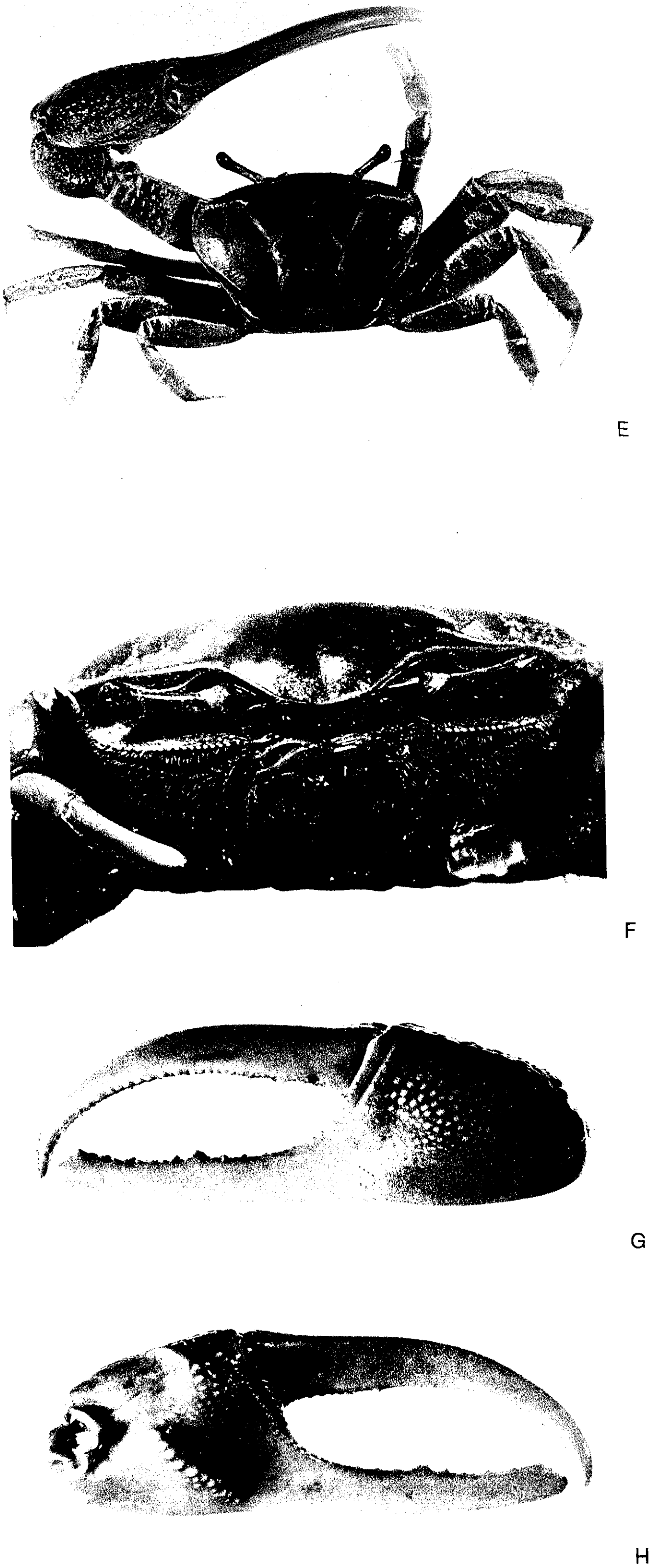


PL. 24. *A-D*. *Uca* (*Minuca*) *vocator vocator*. West Indies: Trinidad (Caroni Swamp). Carapace lgth. 17.5 mm. Leptochelous form. NYZS. (P.166.)

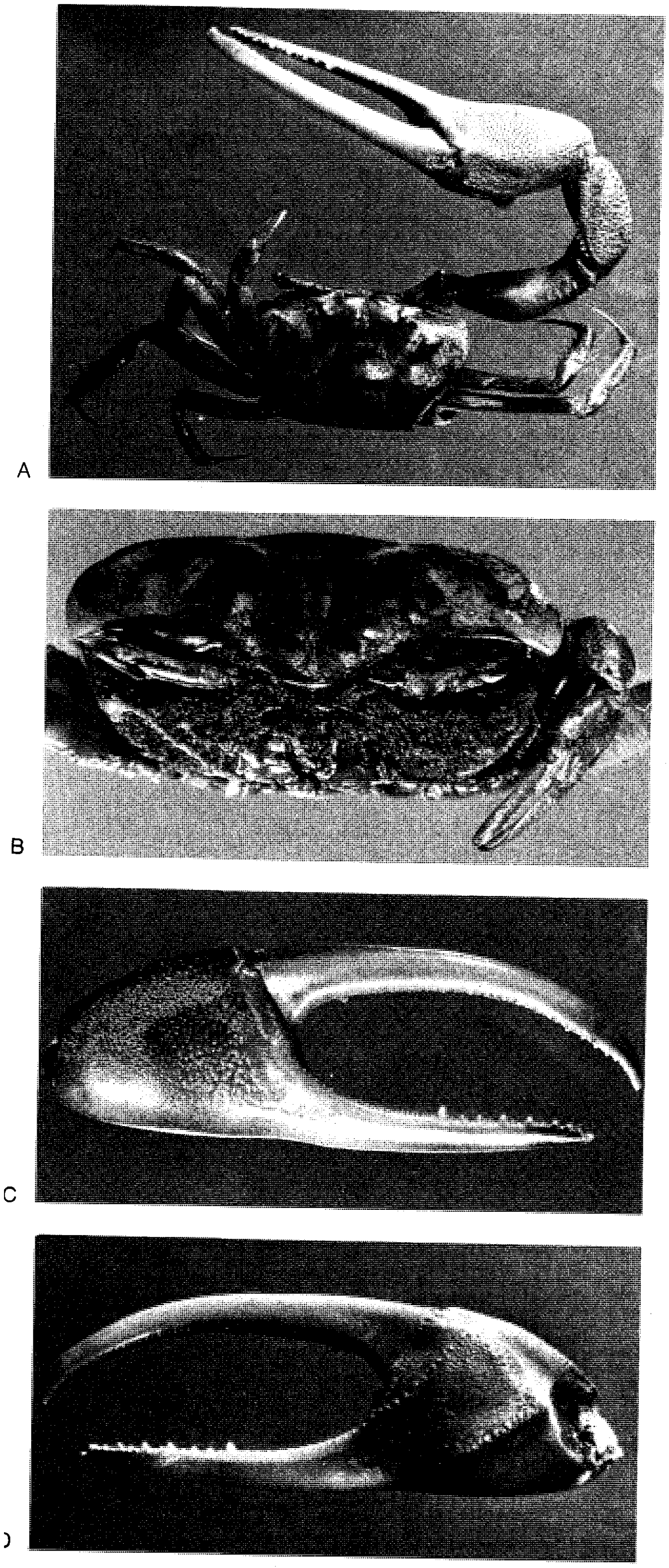
E-H. *Uca* (*Minuca*) *burgersi*. West Indies: Tobago. Carapace lgths.: *E*, *F*, 9 mm; *G*, *H*, 10.5 mm. NYZS. (P. 168.)

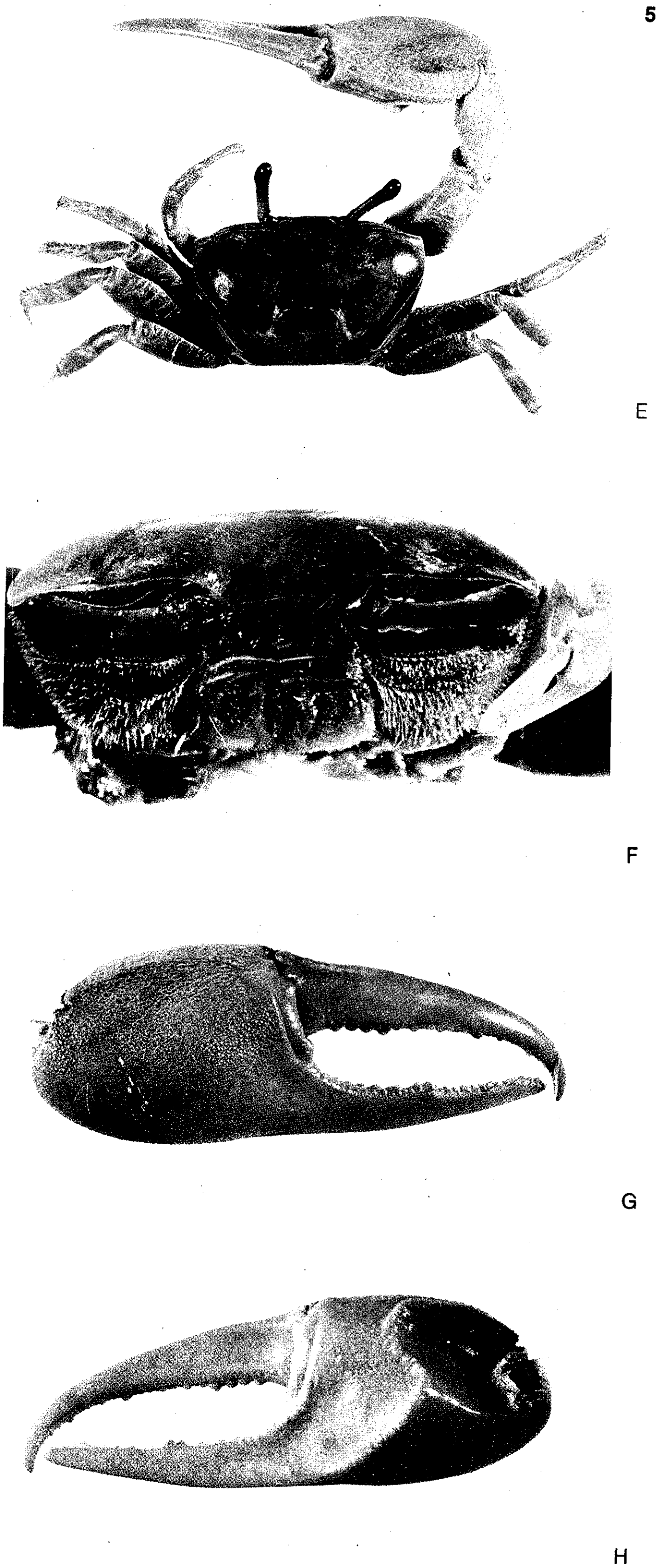


Pl. 25. *A-D. Uca* (*Minuca*) *mordax*. Brazil: Belém. Carapace lgths.: *A*, *B*, 13.5 mm; *C*, *D*, 13 mm. NYZS. (P. 173.)



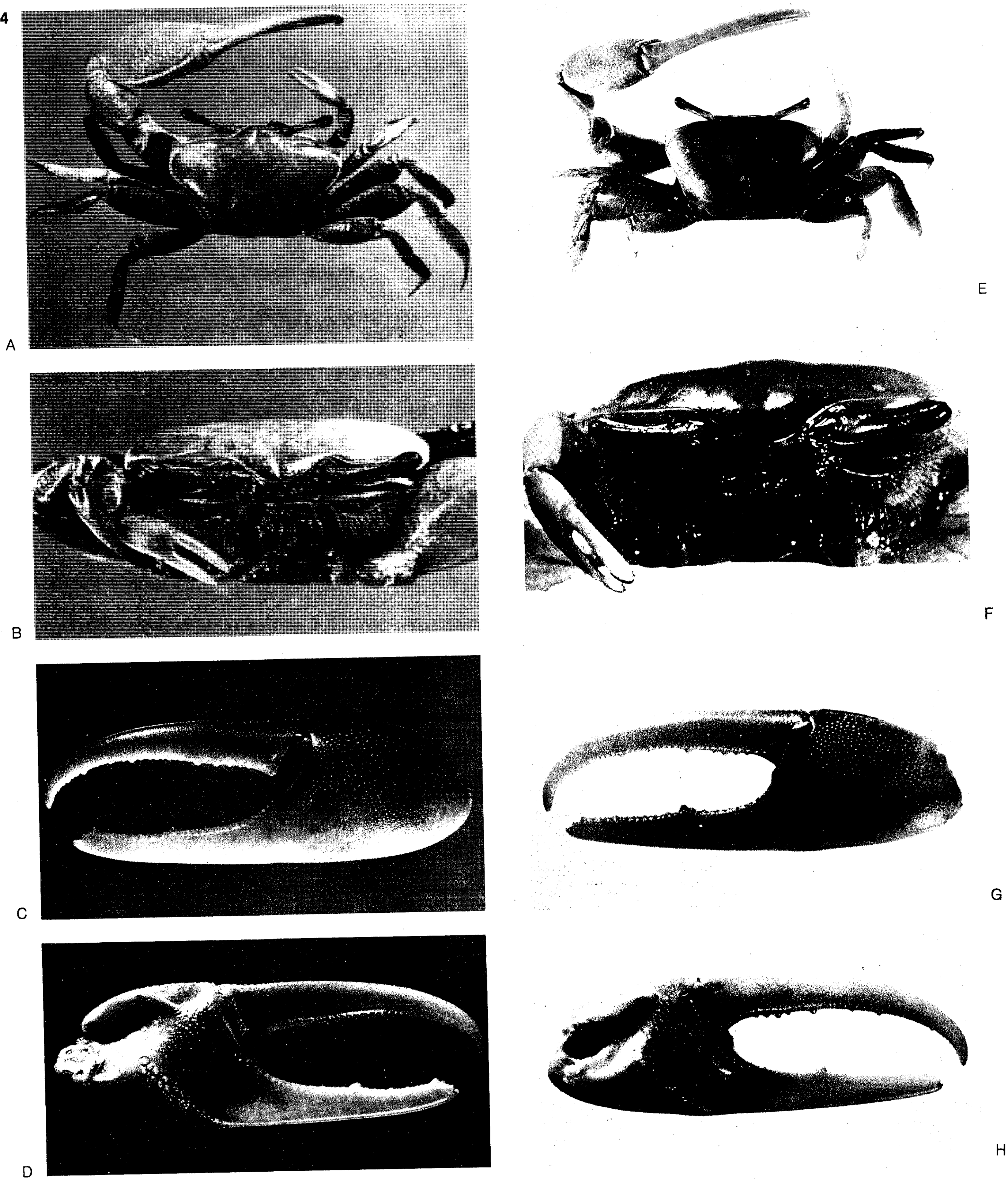
E-H. Uca (*Minuca*) *minax*. United States: New Jersey (near Quinton). Carapace lgth. 28 mm. NYZS. (P. 176.)





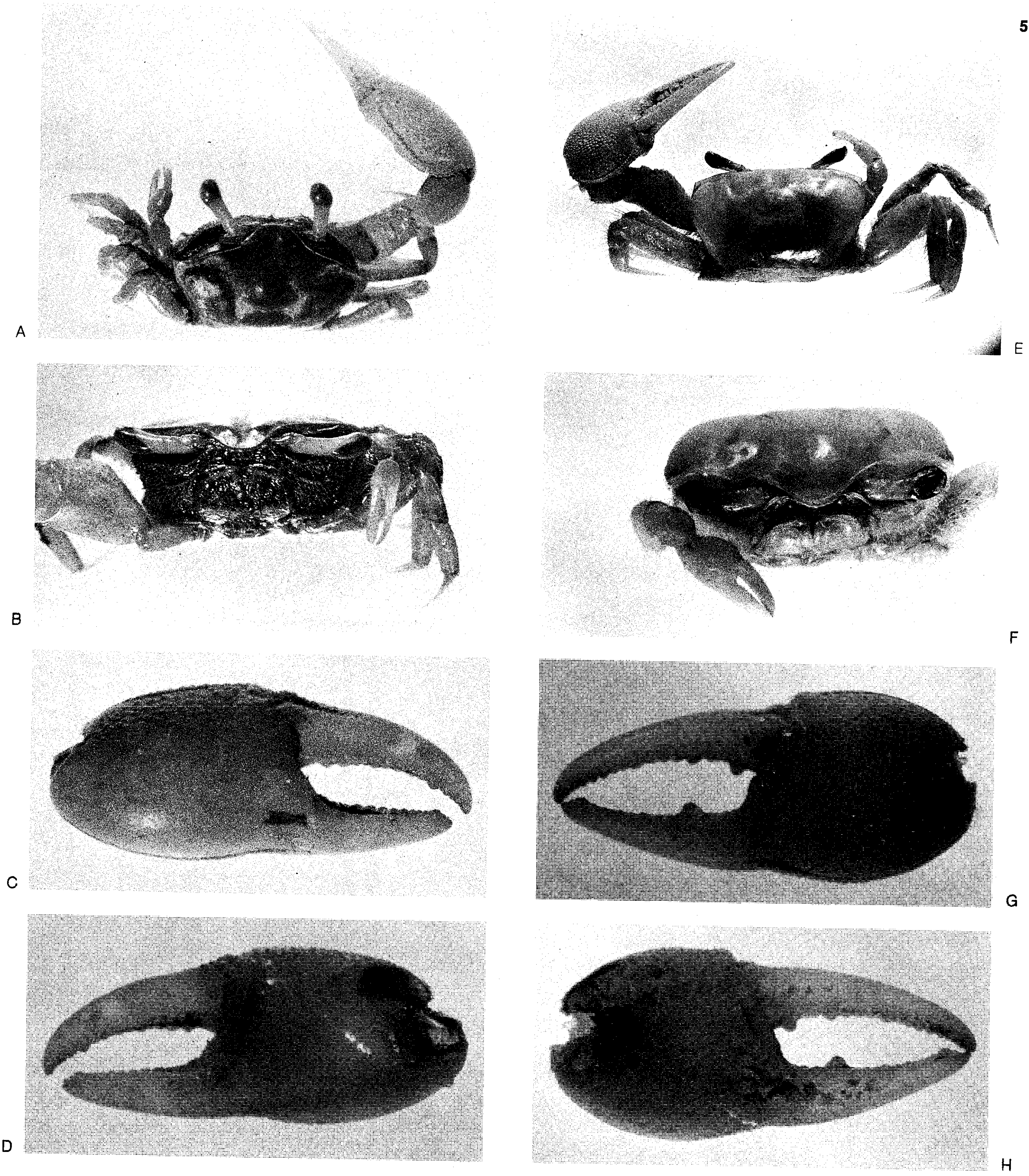
PL. 26. *A-D. Uca* (*Minuca*) *brevifrons.* Eastern Pacific: Panama (Piñas R.). Carapace lgth. 14 mm. AMNH 10702. (P. 180.)

E-H. Uca (*Minuca*) *galapagensis galapagensis.* Eastern Pacific: Ecuador (Guayaquil). Carapace lgth. 14.5 mm. NYZS. (P. 187.)



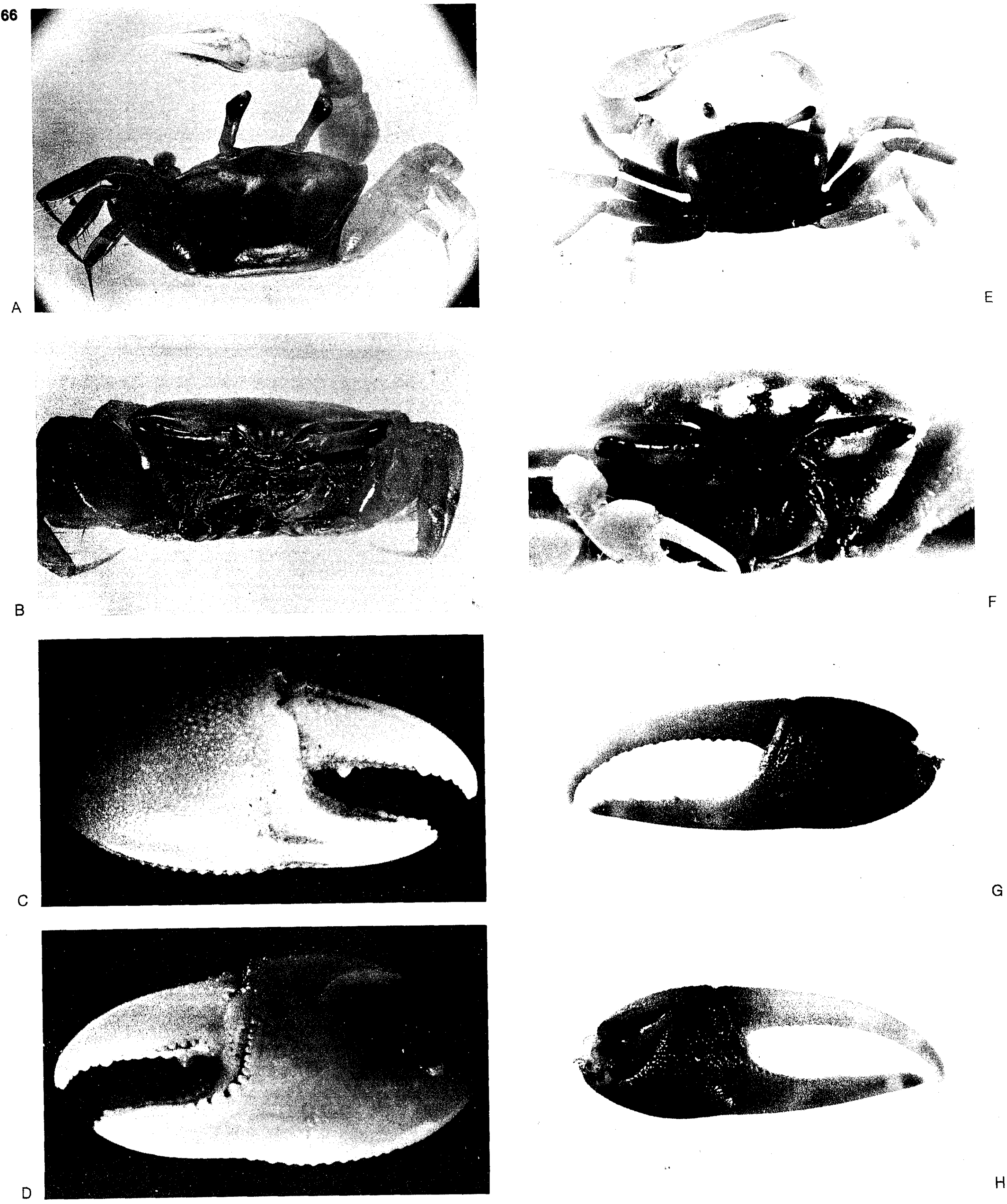
Pl. 27. *A-D*. *Uca* (*Minuca*) *rapax rapax*. West Indies: Trinidad (Cocorite Swamp). Carapace lgth. 12 mm. NYZS. (P. 196.)

E-H. *Uca* (*Minuca*) *pugnax pugnax*. United States: New York (Oyster Bay). Carapace lgth. 12 mm. NYZS. (P. 203.)



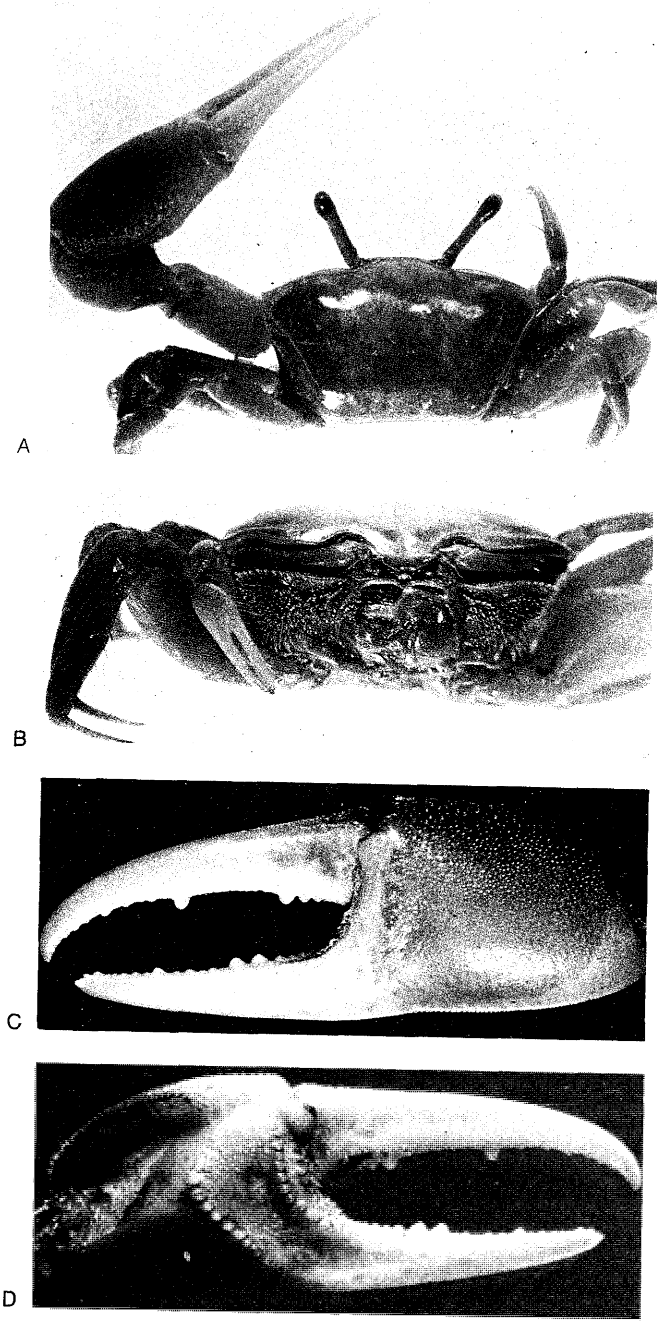
Pl. 28. *A-D. Uca* (*Minuca*) *zacae*. Eastern Pacific: Costa Rica (Golfito). Carapace lgth. 6 mm. NYZS. (P. 206.)

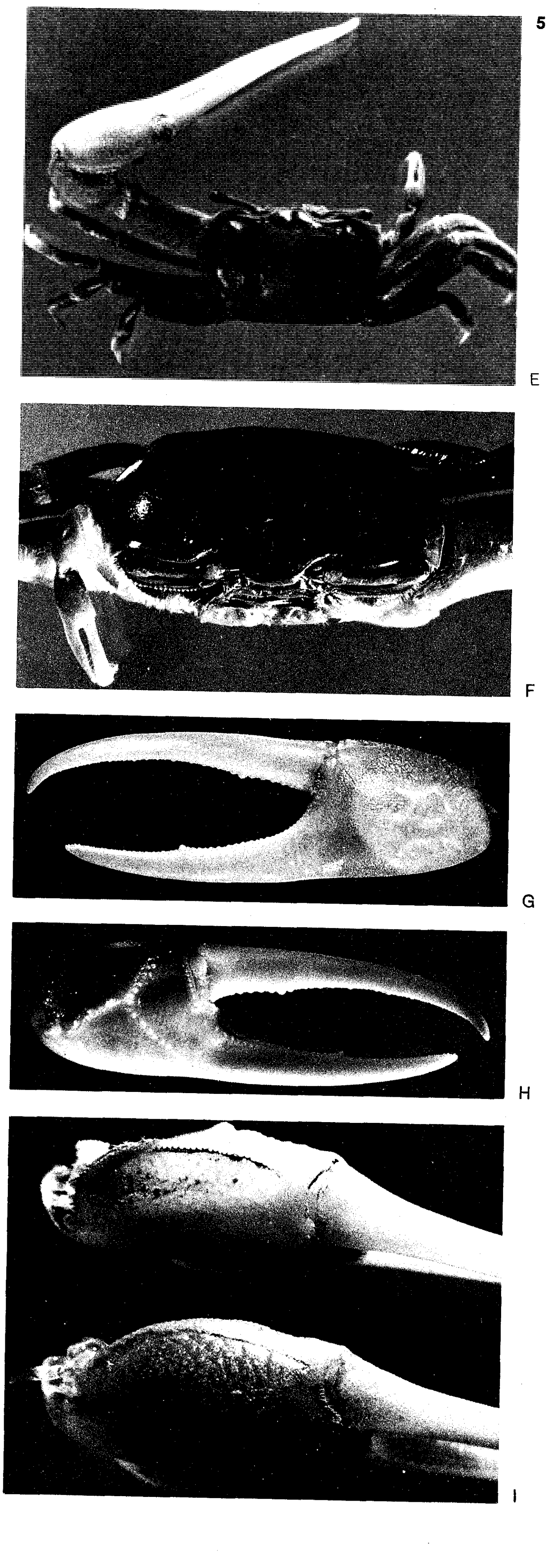
E-H. Uca (*Minuca*) *subcylindrica*. United States: Texas, Carapace lgth. 9 mm. USNM 99826. (P. 209.)



Pl. 29. *A-D. Uca* (*Celuca*) *argillicola.* Eastern Pacific: Panama (Pearl Is.). Carapace lgth. 9 mm. (P. 220.)

E-H. Uca (*Celuca*) *pugilator.* United States: Florida (near Daytona Beach). Carapace lgth. 13 mm. NYZS. (P. 223.)

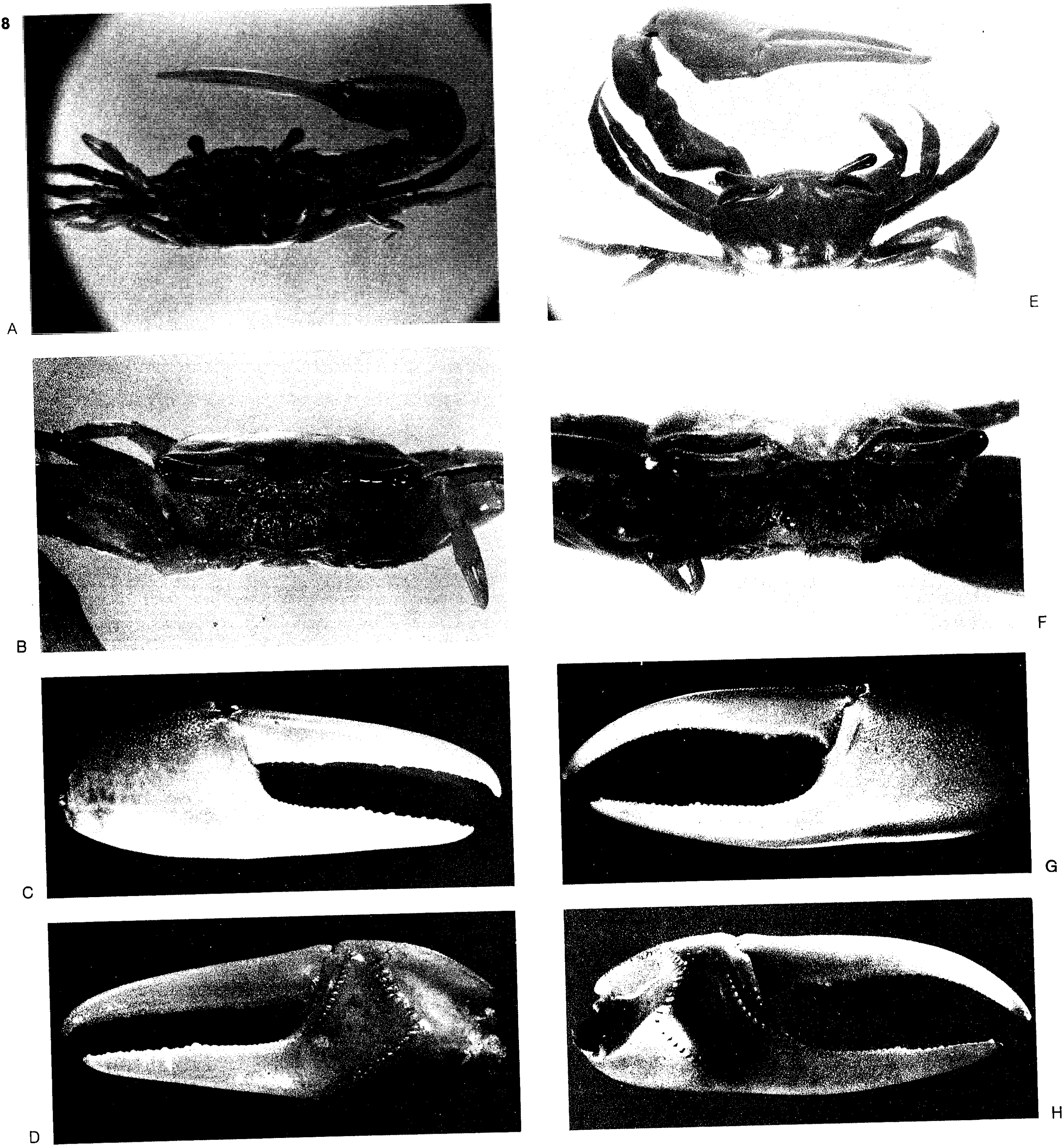




PL. 30. *A-D*. *Uca* (*Celuca*) *uruguayensis*. Uruguay: Maldonado. Carapace lgth. 8 mm. MCZ 5926. (P. 229.)

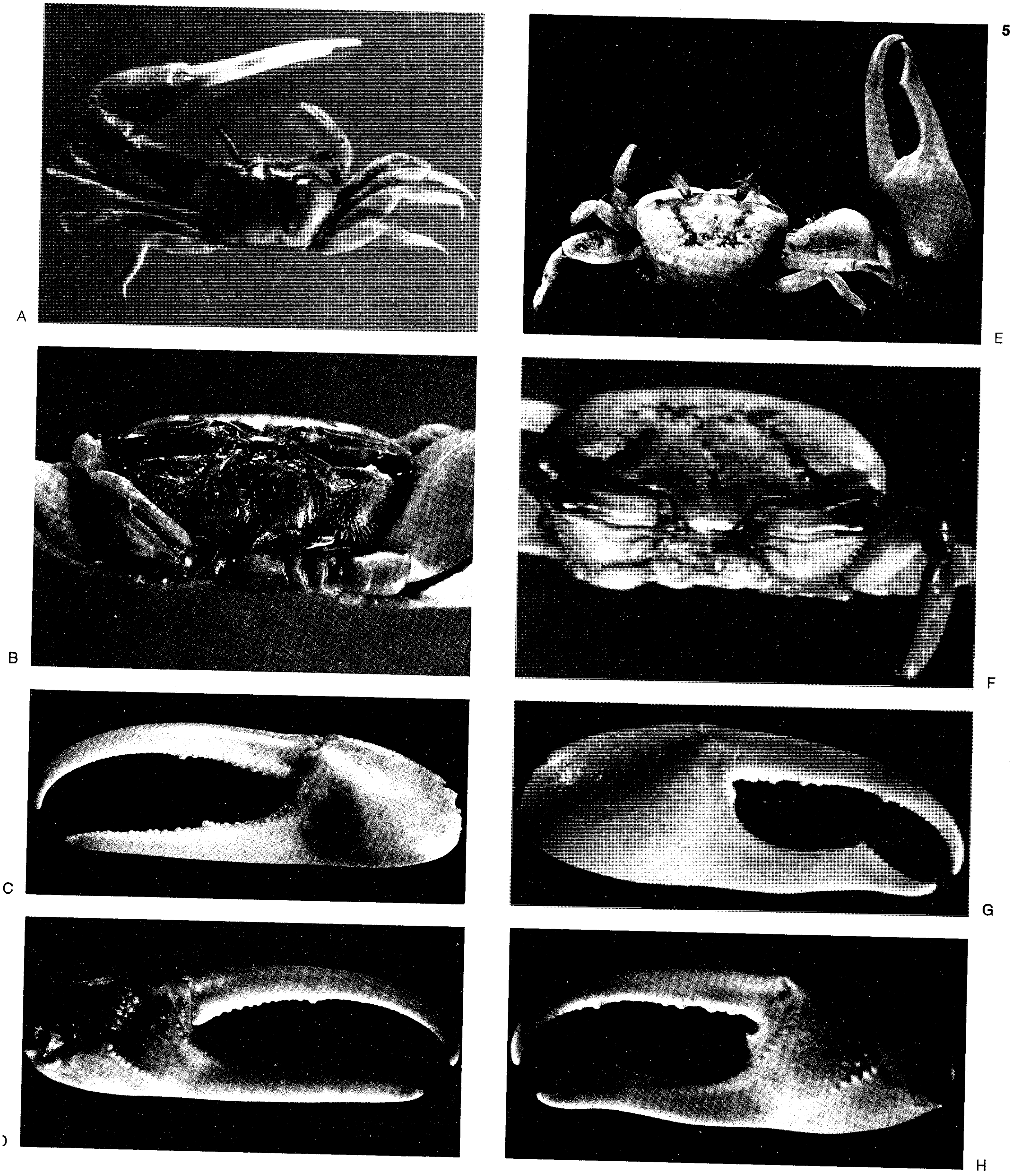
E-H. *Uca* (*Celuca*) *crenulata crenulata*. Mexico: Lower California, west coast (Todos Santos Bay). Carapace lgths.: *E*, *F*, 12 mm.; *G*, *H*, 11 mm. USNM 19033. (P. 234.)

I. Upper: *Uca* (*Celuca*) *crenulata coloradensis*. Mexico: Gulf of California, near mouth of Colorado R. Carapace lgth. 11 mm. USNM 18292. (P. 234.)
Lower: *Uca* (*Celuca*) *crenulata crenulata*. Mexico: Lower California, west coast (Todos Santos Bay). Carapace lgth. 10.5 mm. USNM 19033. (P. 234.)
Obliquely dorsal view of major manus and dactyl in each subspecies.



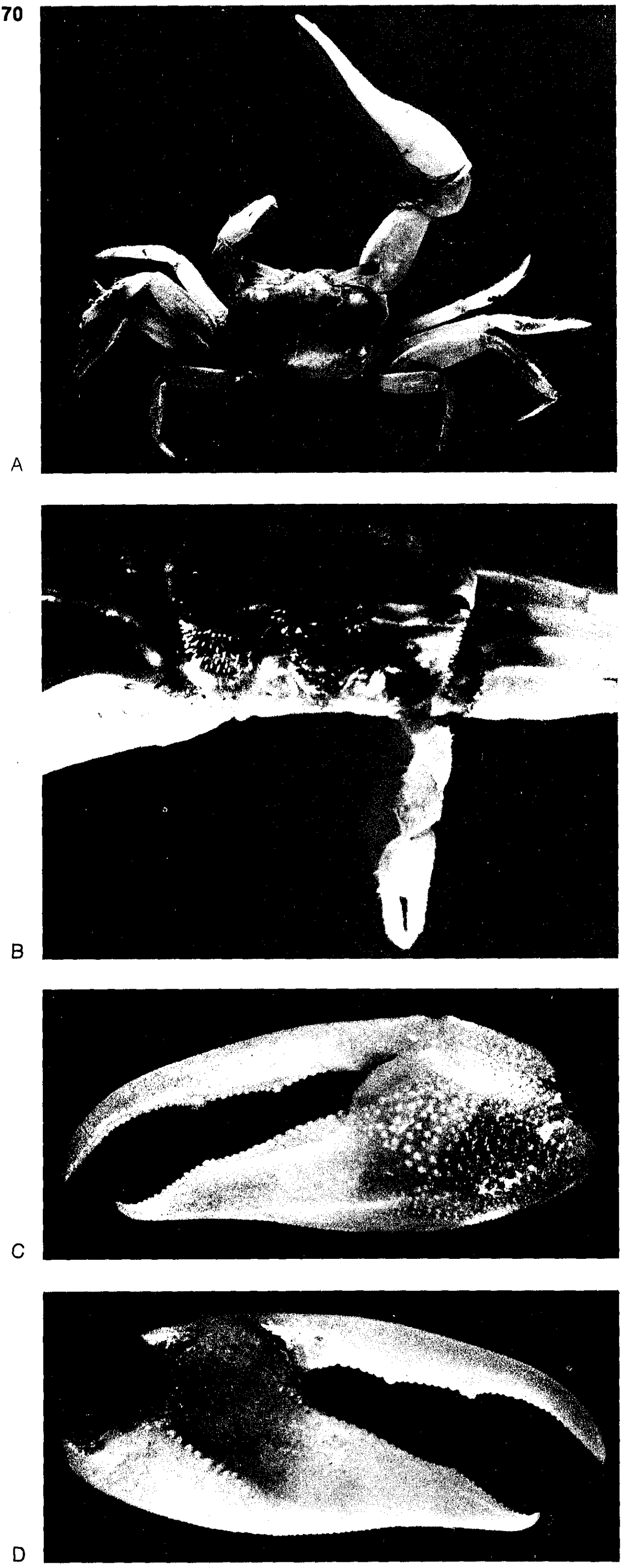
Pl. 31. *A-D. Uca* (*Celuca*) *speciosa speciosa.* United States: Florida (Miami). Carapace lgth. 8 mm. NYZS. (P. 238.)

E-H. Uca (*Celuca*) *speciosa spinicarpa.* United States: Mississippi. Carapace lgth. 11 mm. USNM 90305. (P. 239.)



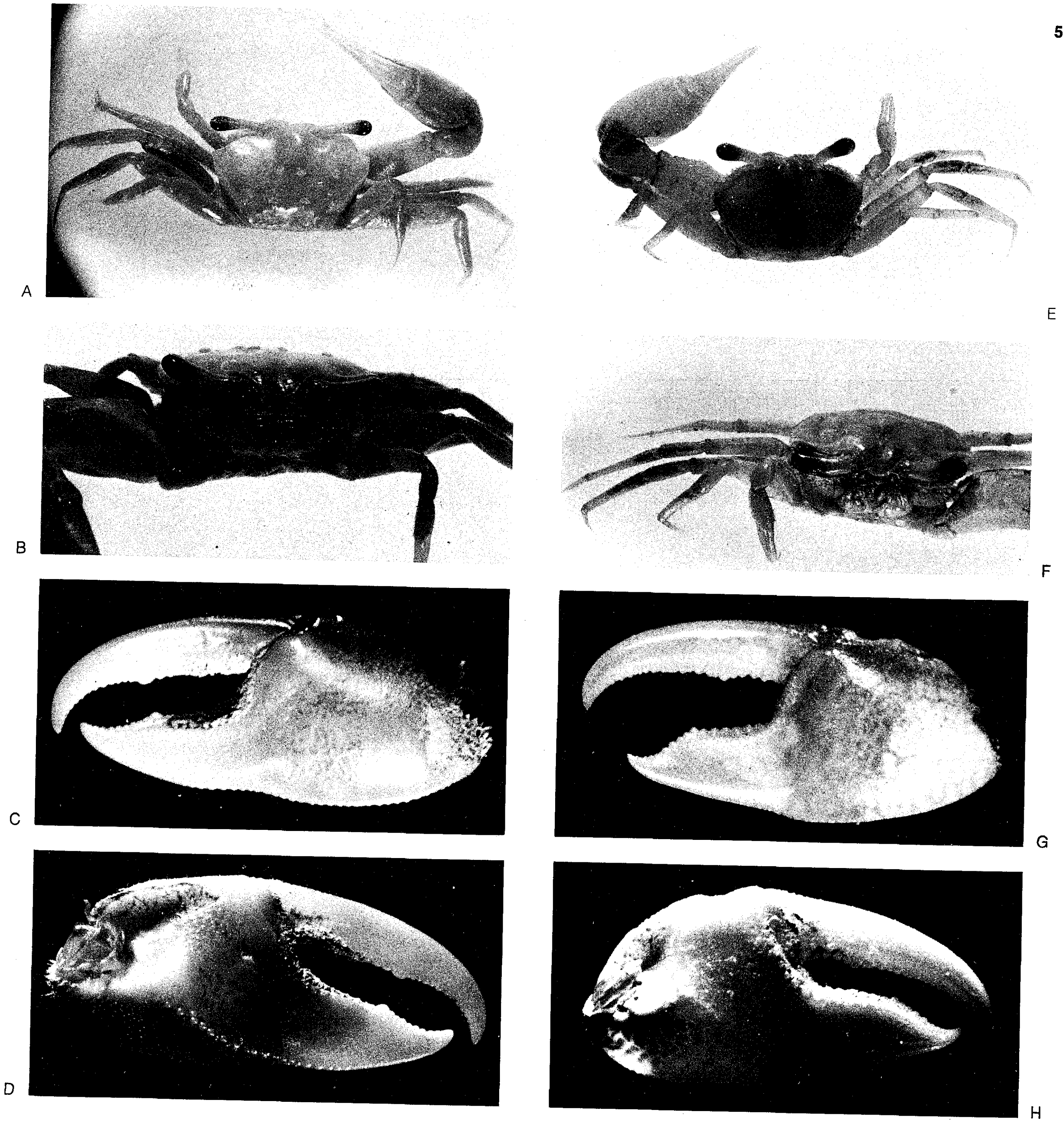
PL. 32. *A-D. Uca* (*Celuca*) *cumulanta.* West Indies: Trinidad (Diego Martin). Carapace lgths.: *A*, *B*, 8.5. mm; *C*, *D*, 9 mm. NYZS. (P. 240.)

E-H. Uca (*Celuca*) *batuenta.* Eastern Pacific: Panama Canal Zone (Balboa). Carapace lgth. ca. 4.5 mm. NYZS 4122 = USNM 137406; paratype. (P. 244.)



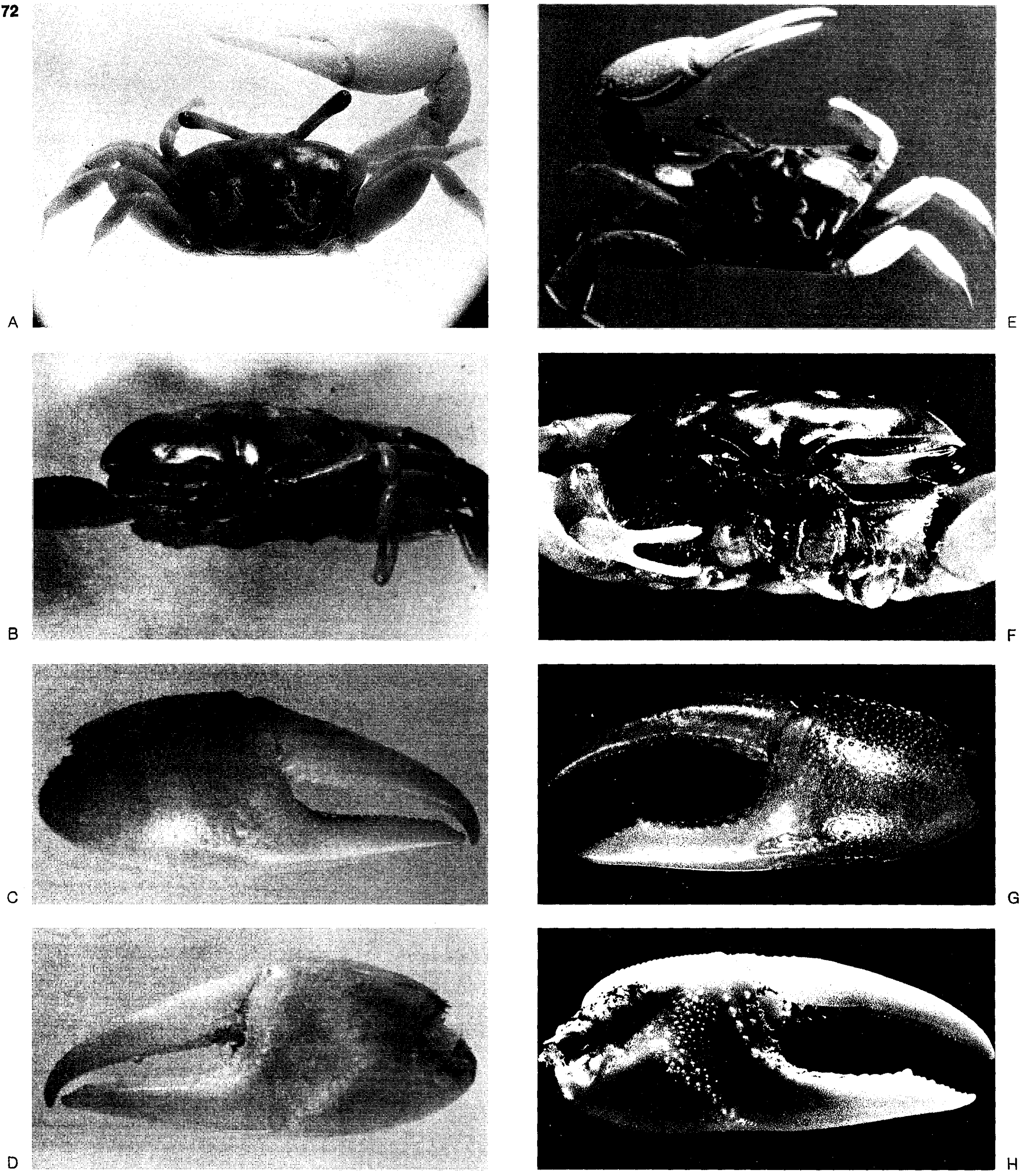
Pl. 33. *A-D*. *Uca* (*Celuca*) *saltitanta*. Eastern Pacific: Panama Canal Zone (Balboa). Carapace lgths.: *A*, *B*, 5.7 mm; *C*, *D*, 5.5 mm. NYZS. (P. 247.)

E-H. *Uca* (*Celuca*) *oerstedi*. Eastern Pacific: Panama (Panama City). Carapace lgth. 6.5 mm. NYZS. (P. 251.)



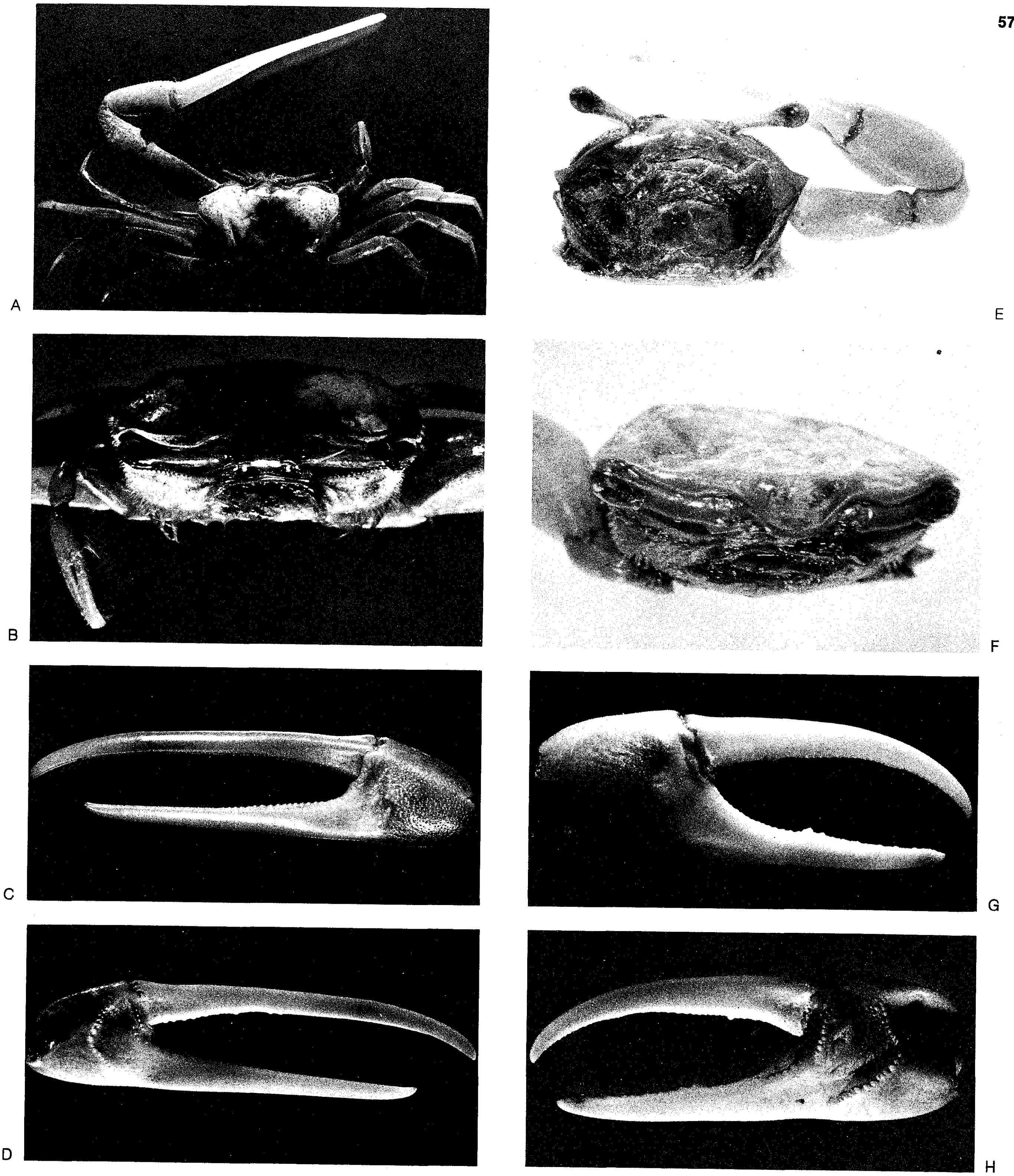
Pl. 34. *A-D*. *Uca* (*Celuca*) *inaequalis*. Eastern Pacific: Ecuador (Guayaquil). Carapace lgths.: *A*, *B*, 6 mm; *C*, *D*, 6.2 mm. NYZS. (P. 254.)

E-H. *Uca* (*Celuca*) *tenuipedis*. Eastern Pacific: Costa Rica (Ballenas Bay). Carapace lgth. 5 mm. NYZS 381,144 = USNM 137410; paratype. (P. 258.)



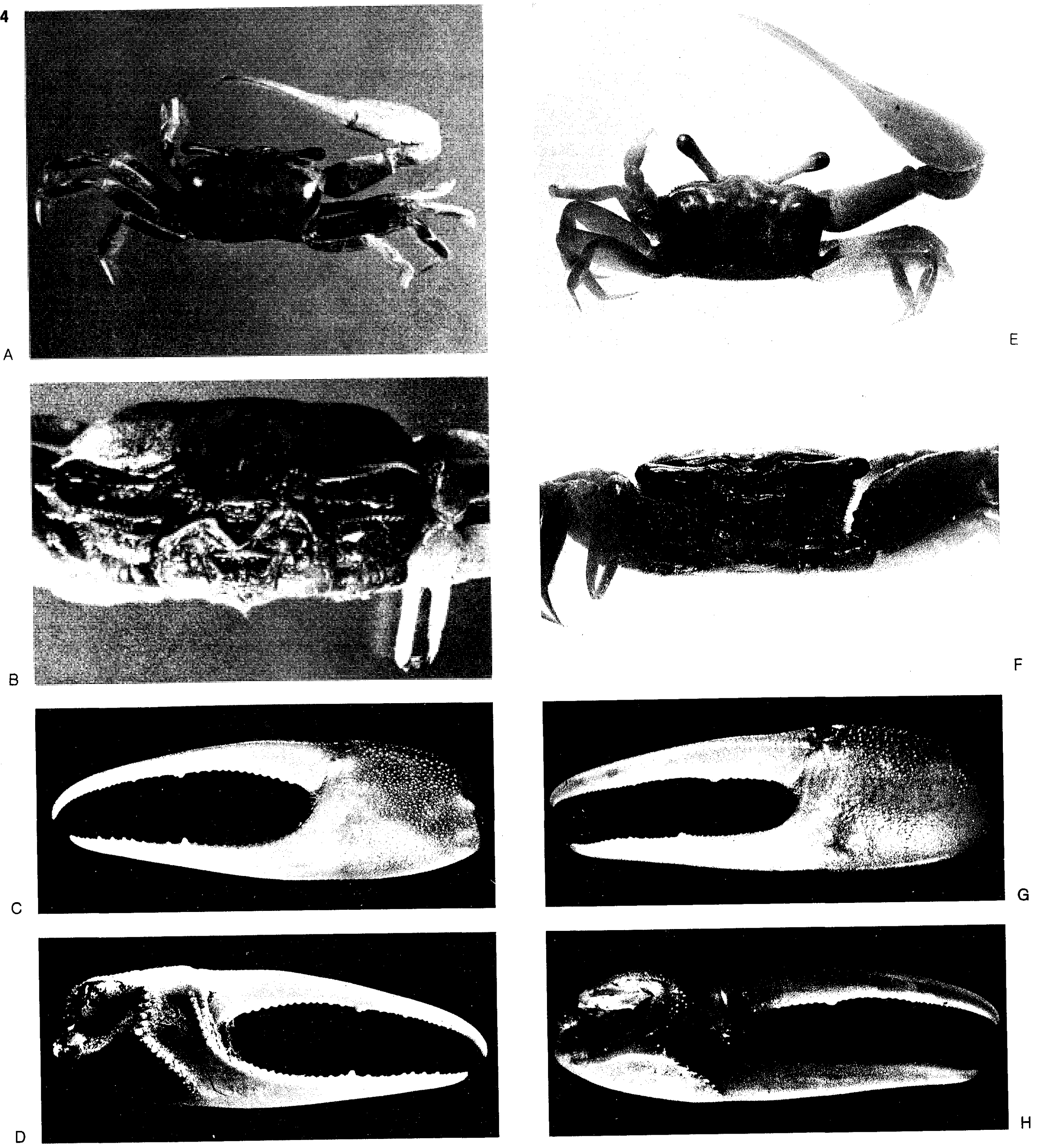
PL. 35. *A-D*. *Uca* (*Celuca*) *tomentosa*. Eastern Pacific: Costa Rica (Puntarenas). Carapace lgth. 6.6 mm. NYZS 381,132 = USNM 137411; holotype. (P. 261.)

E-H. *Uca* (*Celuca*) *tallanica*. Eastern Pacific: Ecuador (Puerto Bolivar). Carapace lgth. 7 mm. NYZS. (P. 264.)



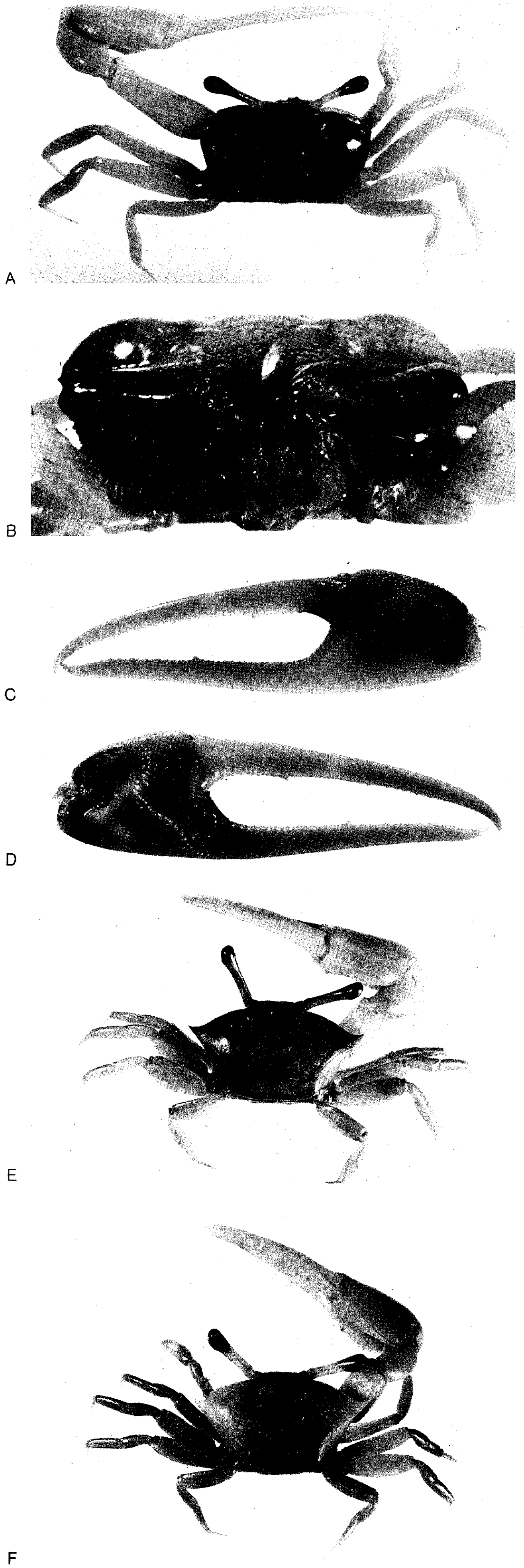
Pl. 36. *A-D. Uca (Celuca) festae.* Eastern Pacific: Ecuador (Guayaquil). Carapace lgths. *A, B,* 7.2 mm; *C, D,* 8 mm. NYZS. (P. 267.)

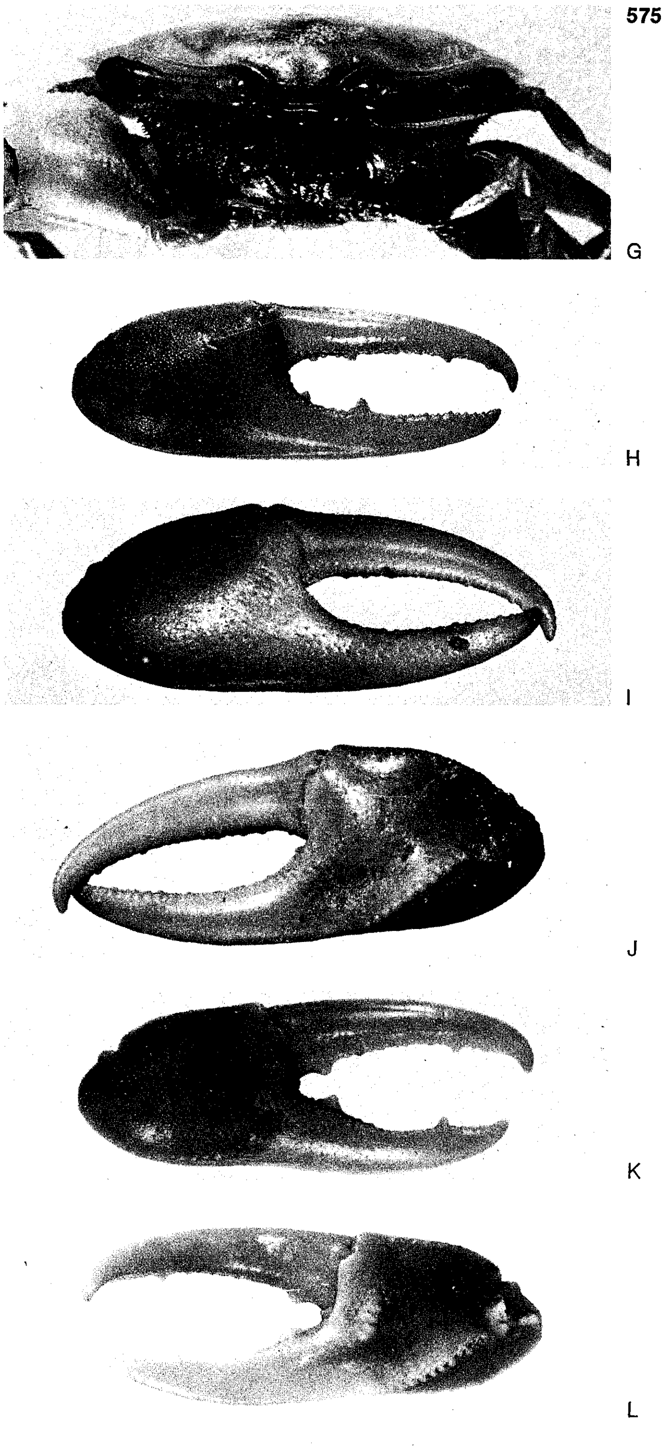
E-H. Uca (Celuca) helleri. Eastern Pacific: Galapagos Is. Carapace lgth. 6.8 mm. USNM 25666. (P. 271.)



Pl. 37. *A-D*. *Uca* (*Celuca*) *dorotheae*. Eastern Pacific: Ecuador (Puerto Bolivar). Carapace lgths.: *A*, *B*, 7 mm; *C*, *D*, 8 mm. NYZS. (P. 275.)

E-H. *Uca* (*Celuca*) *beebei*. Eastern Pacific: Panama (Panama City). Carapace lgth. 5.5 mm. NYZS. (P. 278.)





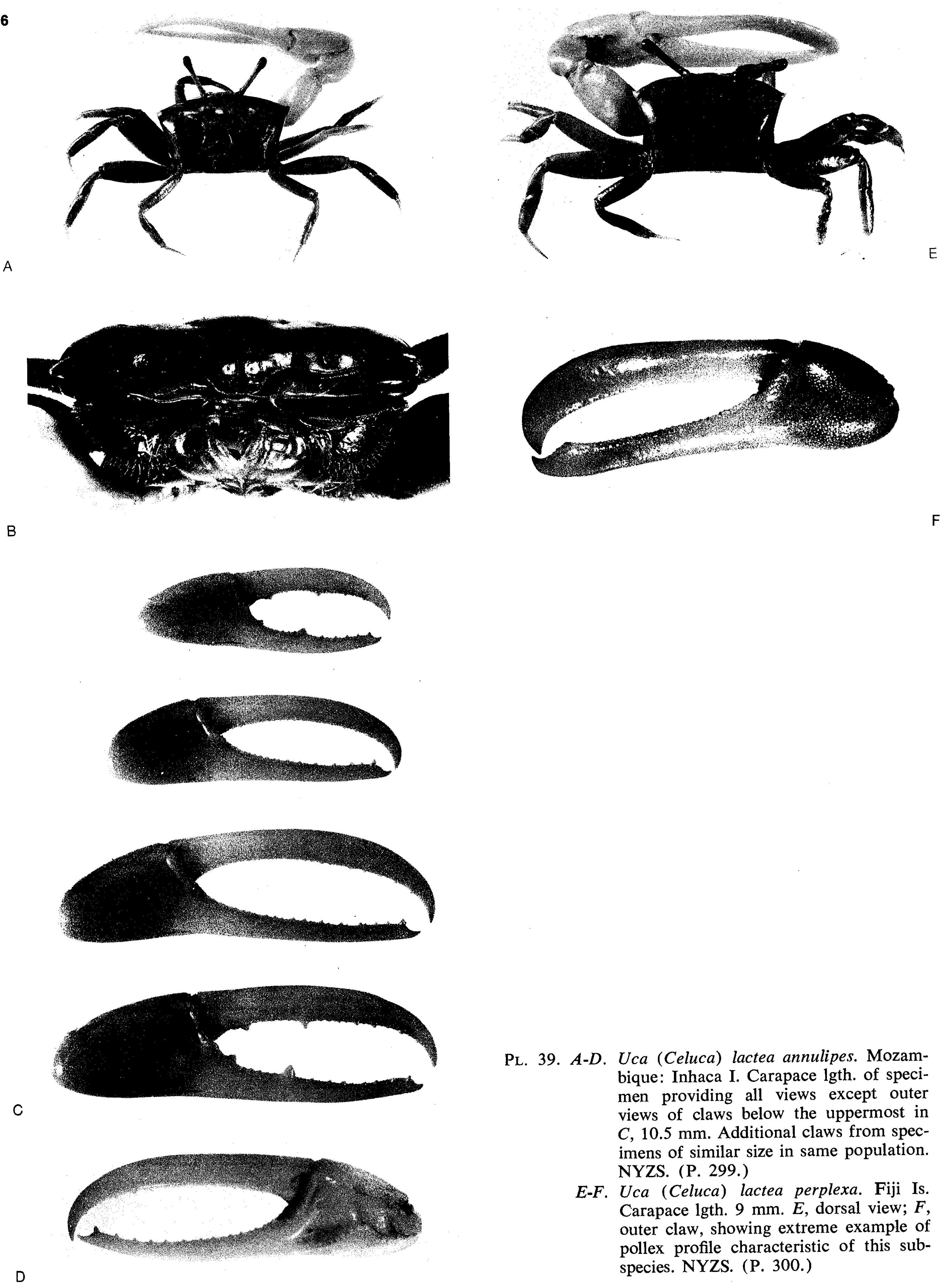
Pl. 38. *A-D.* *Uca* (*Celuca*) *stenodactylus.* Eastern Pacific: Nicaragua (Corinto). Carapace lgth. 7.5 mm. NYZS. (P. 282.)

E. *Uca* (*Celuca*) *triangularis bengali.* Malaya: Penang. Carapace lgth. 7 mm. Dorsal view. NYZS. (P. 290.)

F-H. *Uca* (*Celuca*) *triangularis triangularis.* Philippine Is.: Madaum. Carapace lgth. 7 mm. *H*, outer claw. NYZS. (P. 290.)

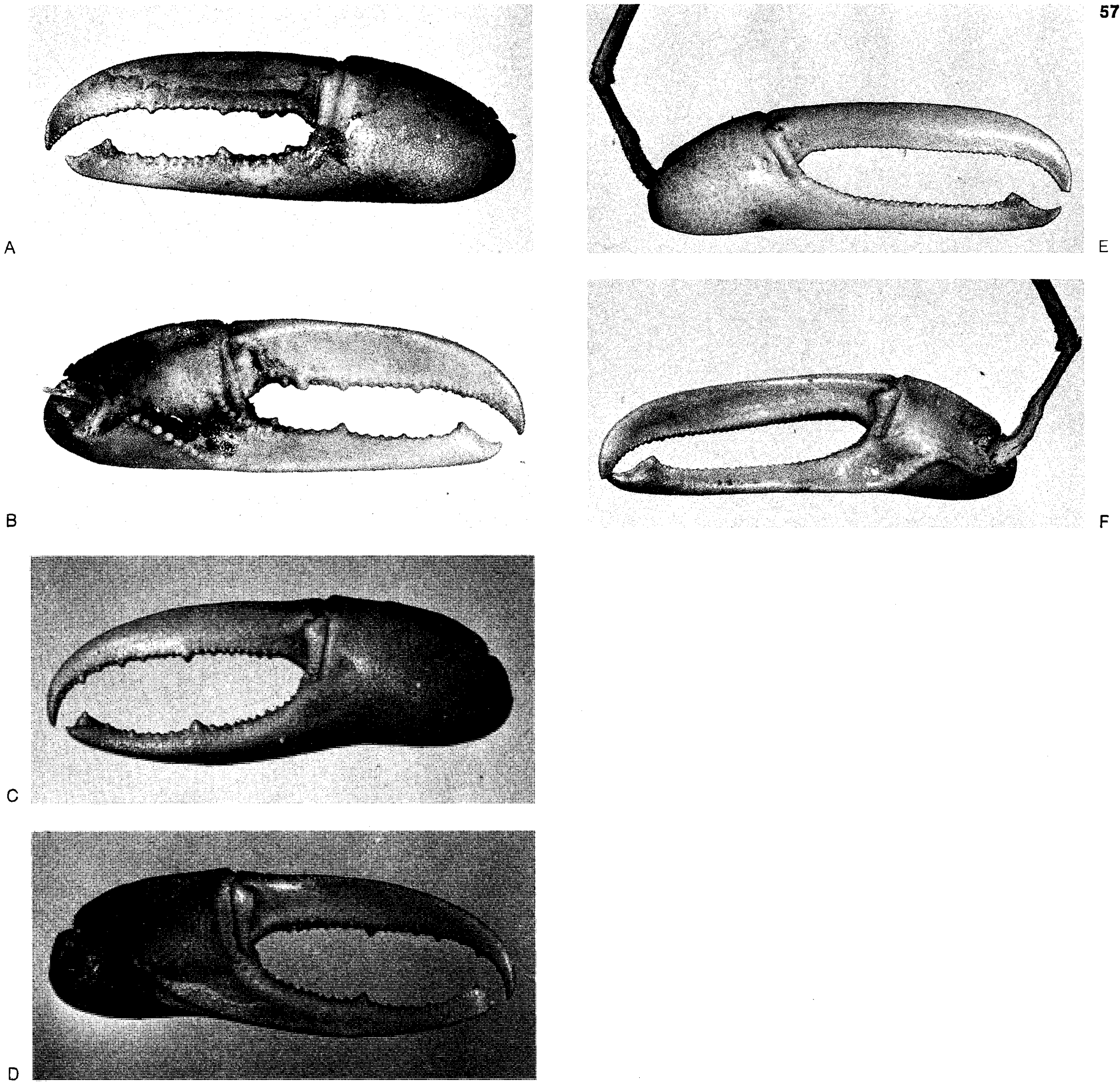
I-J. *Uca* (*Celuca*) *triangularis triangularis.* New Caledonia. Carapace lgth. 8 mm. Paris: "type non specifié" of *Gelasimus triangularis*; claw. (P. 289.)

K-L. *Uca* (*Celuca*) *triangularis bengali.* Claw. Other data as in *E.*



Pl. 39. *A-D*. *Uca* (*Celuca*) *lactea annulipes*. Mozambique: Inhaca I. Carapace lgth. of specimen providing all views except outer views of claws below the uppermost in *C*, 10.5 mm. Additional claws from specimens of similar size in same population. NYZS. (P. 299.)

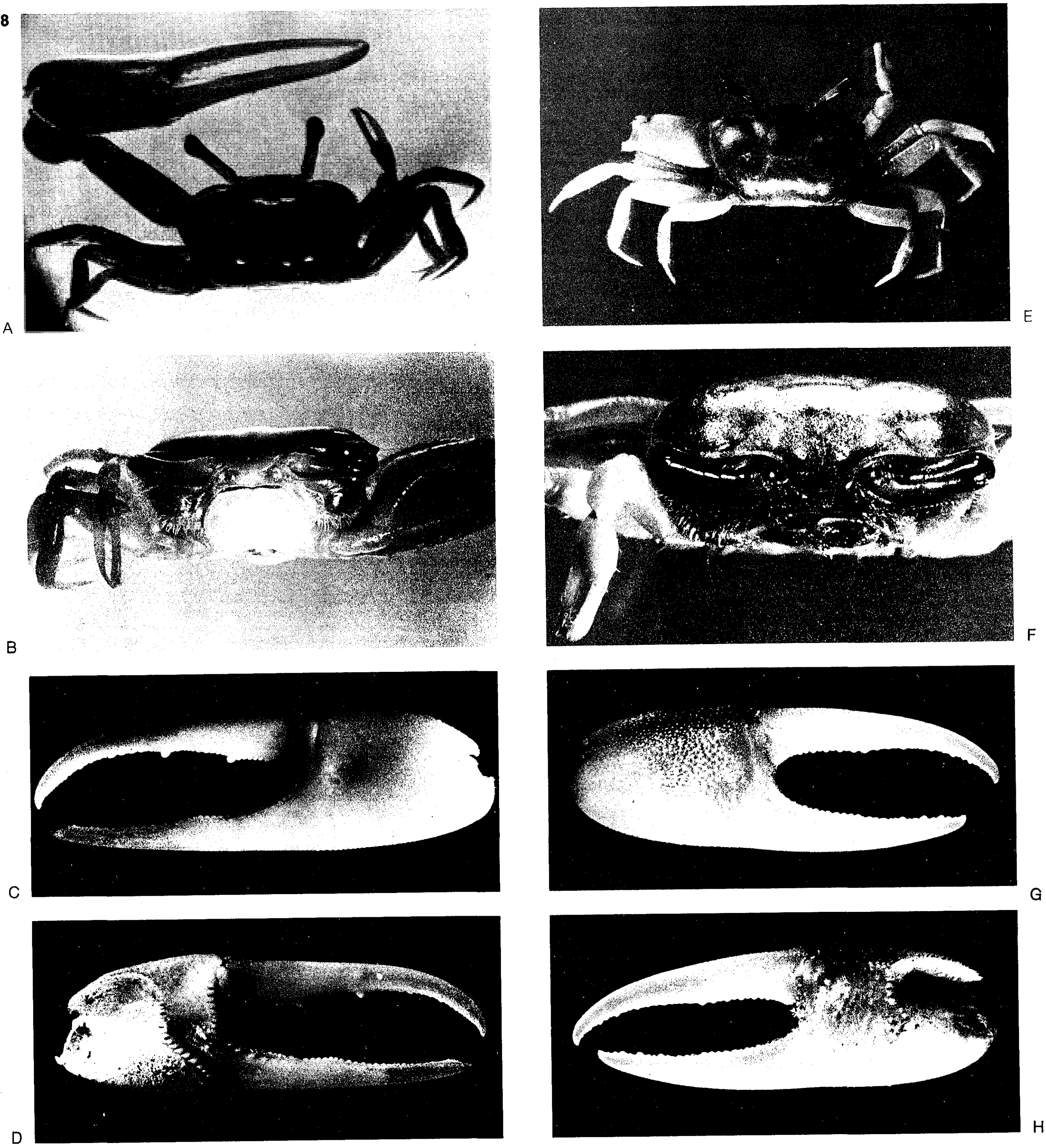
E-F. *Uca* (*Celuca*) *lactea perplexa*. Fiji Is. Carapace lgth. 9 mm. *E*, dorsal view; *F*, outer claw, showing extreme example of pollex profile characteristic of this subspecies. NYZS. (P. 300.)



Pl. 40. *A-B*. *Uca* (*Celuca*) *lactea lactea*. Japan. Carapace lgth. 11.5 mm. Paris, from Leiden; perhaps a cotype of *Gelasimus lacteus*; claw. (P. 298.)

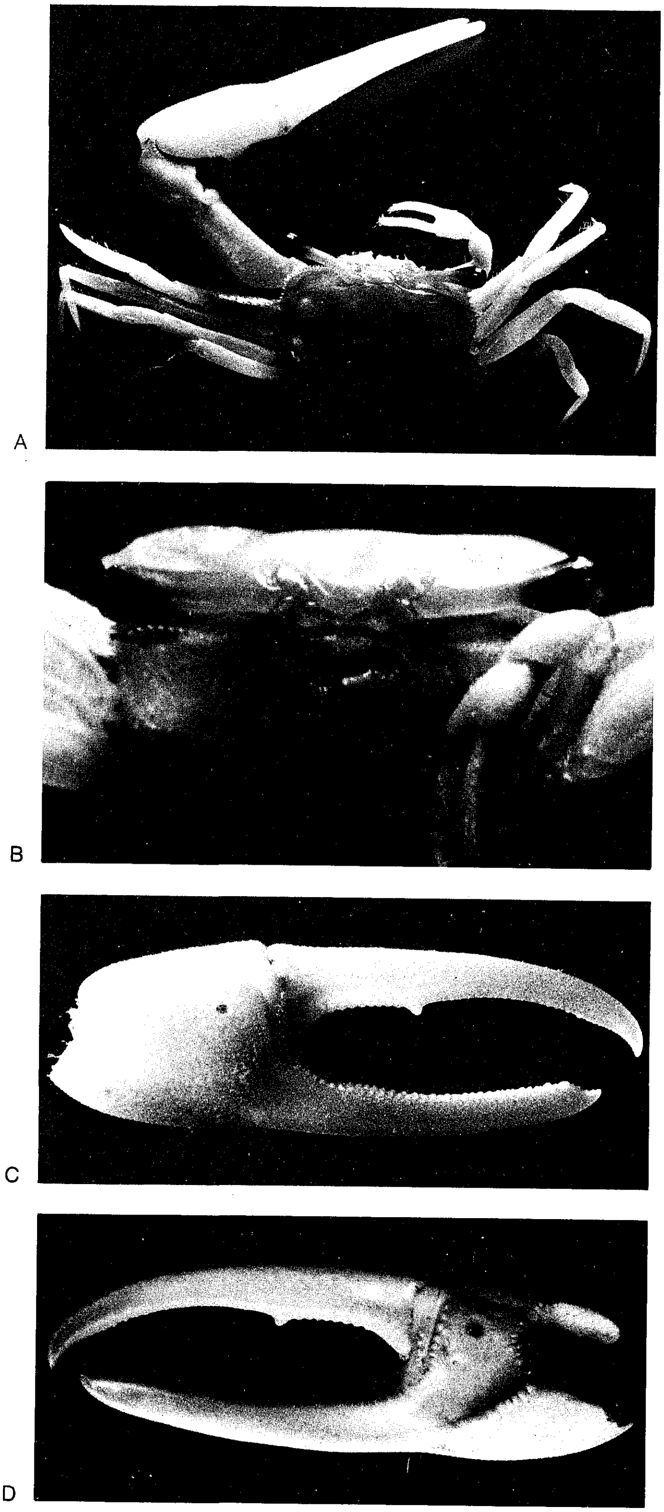
C-D. *Uca* (*Celuca*) *lactea annulipes*. "Mer des Indes." Carapace lgth. 10.5 mm. Paris: lectotype of *Gelasimus annulipes*; claw. (P. 298.)

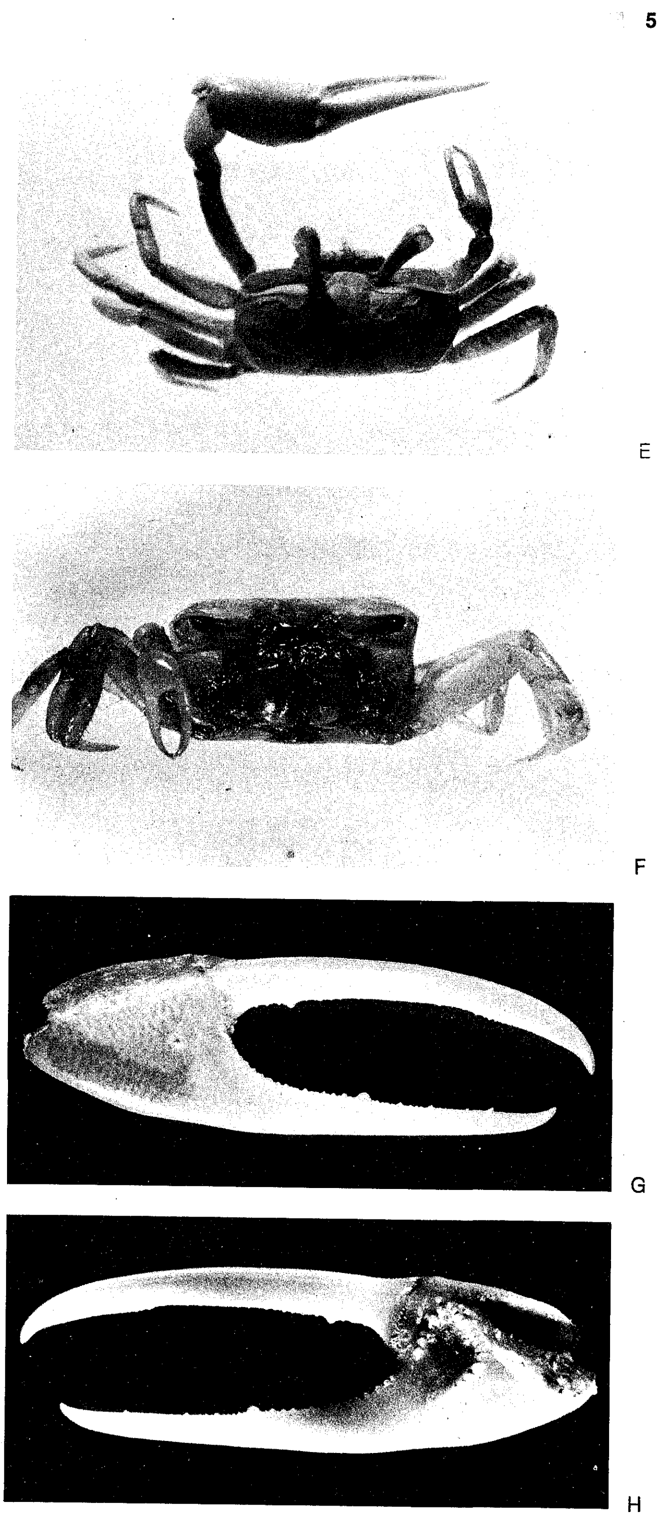
E-F. *Uca* (*Celuca*) *lactea*. Australia. Propodus lgth. 32 mm. Paris: claw of composite type of *Gelasimus forceps*. (P. 298.)



PL. 41. *A-D. Uca (Celuca) leptodactyla.* Venezuela: Turiamo. Carapace lgths.: *A*, *B*, ca. 5.2 mm; *C*, *D*, 5.5 mm. NYZS. (P. 304.)

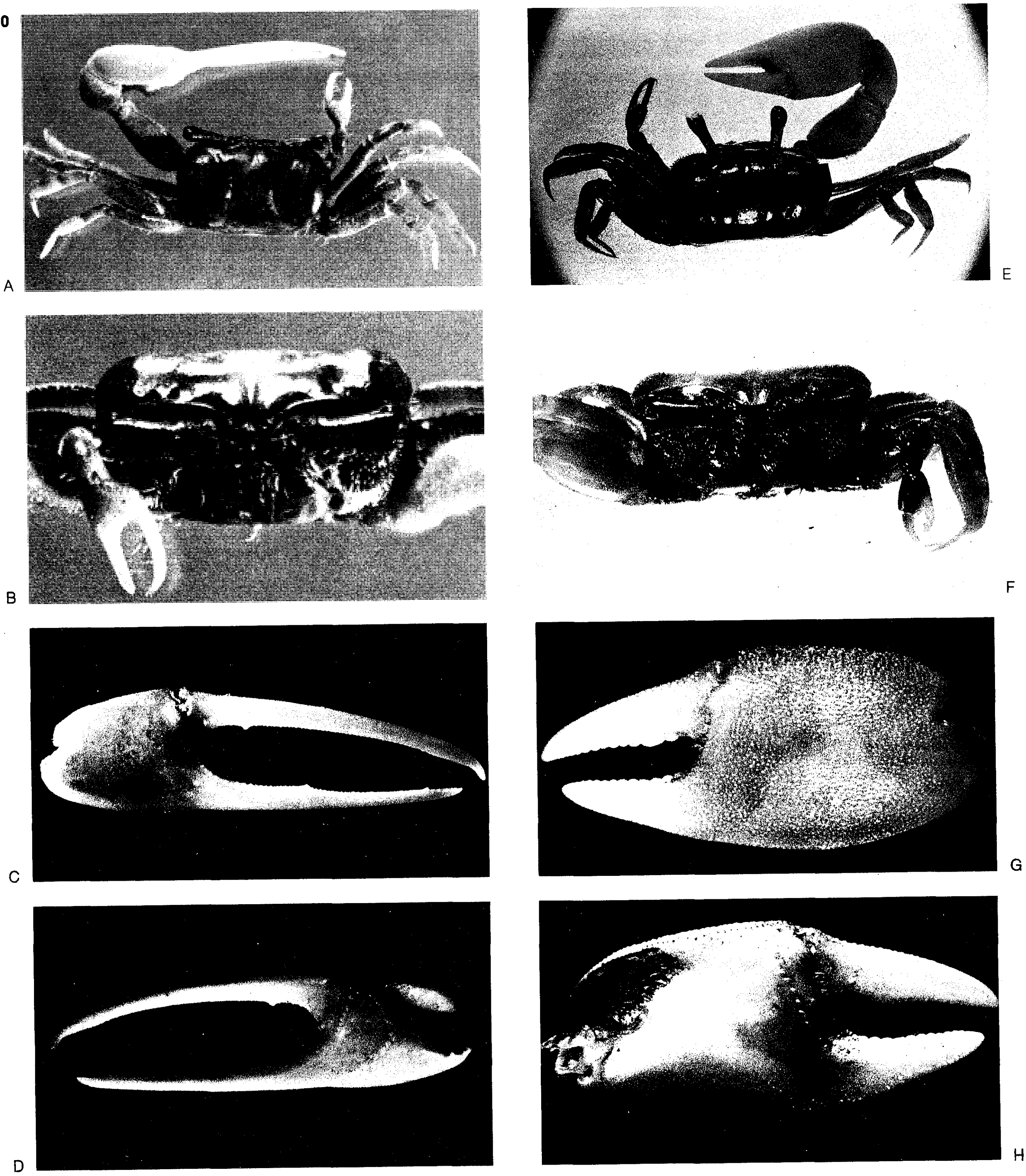
E-H. Uca (Celuca) limicola. Eastern Pacific: Costa Rica (Golfito). Carapace lgths.: *E*, *F*, 6.2 mm; *G*, *H*, 7 mm. NYZS. 381,-153 = USNM 79401; paratypes. (P. 308.)





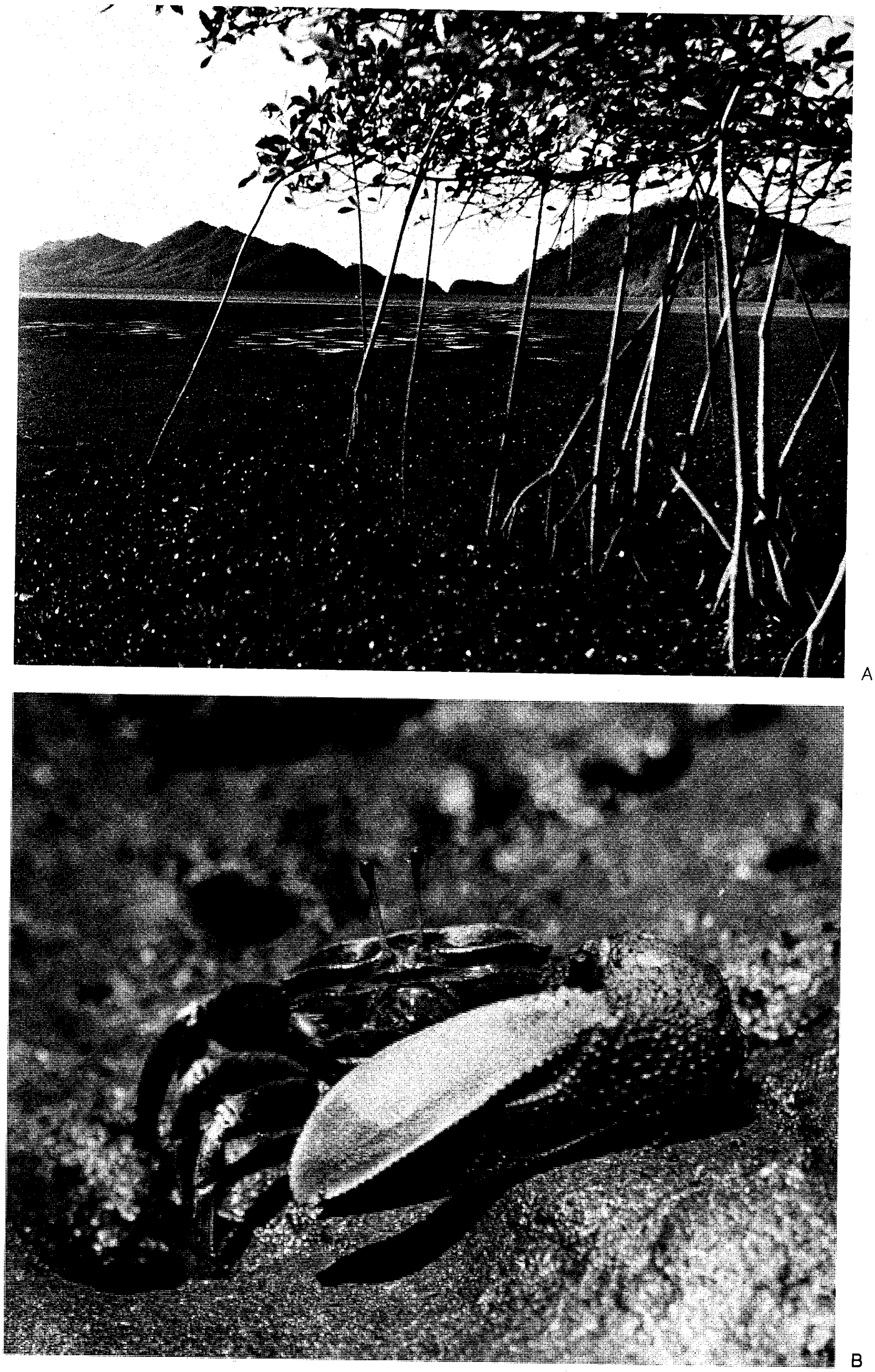
PL. 42. *A-D*. *Uca* (*Celuca*) *deichmanni*. Eastern Pacific: Costa Rica (Golfito). Carapace lgths.: *A*, *B*, 6 mm; *C*, *D*, 6.2 mm. NYZS. (P. 311.)

E-H. *Uca* (*Celuca*) *musica terpsichores*. Eastern Pacific: Costa Rica (Golfito). Carapace lgths.: *E*, *F*, 5.5 mm; *G*, *H*, 6 mm. NYZS. (P. 316.)



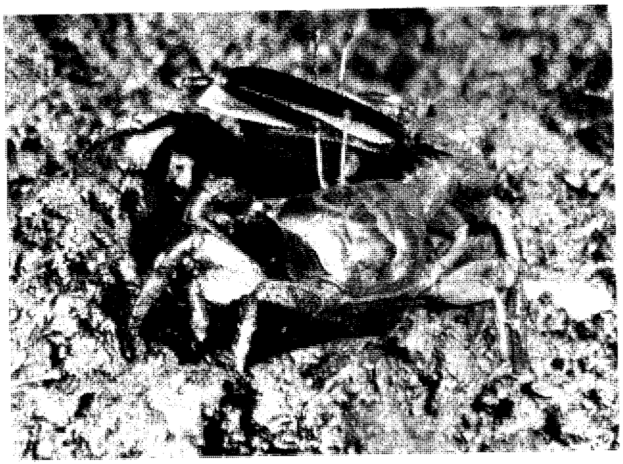
PL. 43. *A-D. Uca (Celuca) musica musica.* Mexico: Gulf of California, east coast (San Blas). Carapace lgths.: *A, B,* 6 mm; *C, D,* 5.8 mm. USNM 99755. (P. 317.)

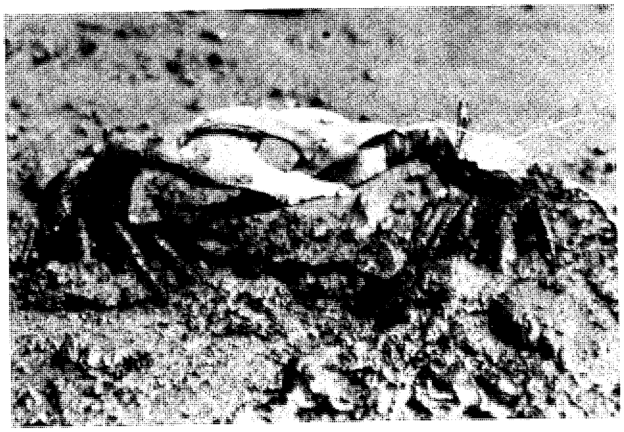
E-H. Uca (Celuca) latimanus. Eastern Pacific: Panama Canal Zone (Balboa). Carapace lgth. 8 mm. NYZS. (P. 319.)

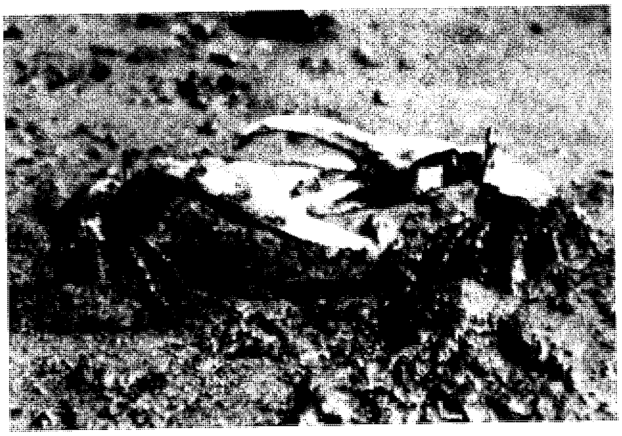


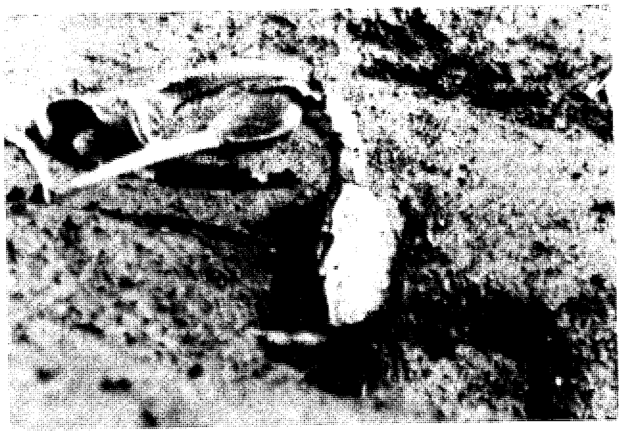
Pl. 44. *A.* One excellent habitat for fiddler crabs: a sheltered bay in the tropics, with a wide tidal range, a beach of sandy mud, and mangroves standing close to the mouth of a stream. Locality: the Pacific coast of Costa Rica, near Port Parker.

B. A living male fiddler crab, *Uca* (*Uca*) *maracoani maracoani*, in Trinidad. (P. 147.)









PL. 45. Combat in *Uca*. (P. 485.) All photographs made from 16 mm color motion picture frames.

A. Low intensity: the manus-push in (*Celuca*) *lactea annulipes* in a combat between two burrow-holders. Singapore.

B. An irregular, forceful fight between a burrow-holder and an aggressive wanderer in (*Uca*) *maracoani maracoani*. Trinidad.

C. High-intensity ritualized combat in (*Minuca*) *rapax rapax*, in Trinidad. Tap following a heel-and-ridge in homoclawed combat. The actor is the crab on the right. His dactyl is striking the heel of his opponent's manus while his pollex is free.

D. Same combat as in *C*. Alternate stroke showing the actor's pollex against his opponent's invisible oblique ridge, on inner side of manus.

E. A heteroclawed combat occurring in the same population, showing the interlace component. The actor is on the right. The teeth near his dactyl's base are starting to rub downward against the ridges of his opponent's inner manus, which parallel the dactyl's base.

F. Same combat as in *E*, near end of the downward stroke.

Pl. 46. Major claws in *Uca*. *A-C*, depressed areas at base of pollex that apparently facilitate seizure by an opponent during forceful combat. *D-F*, healed puncture wounds, apparently received in combat. (P. 515.)

A. (*Deltuca*) *forcipata*; outer claw. Data as in Pl. 6 *A-D*.

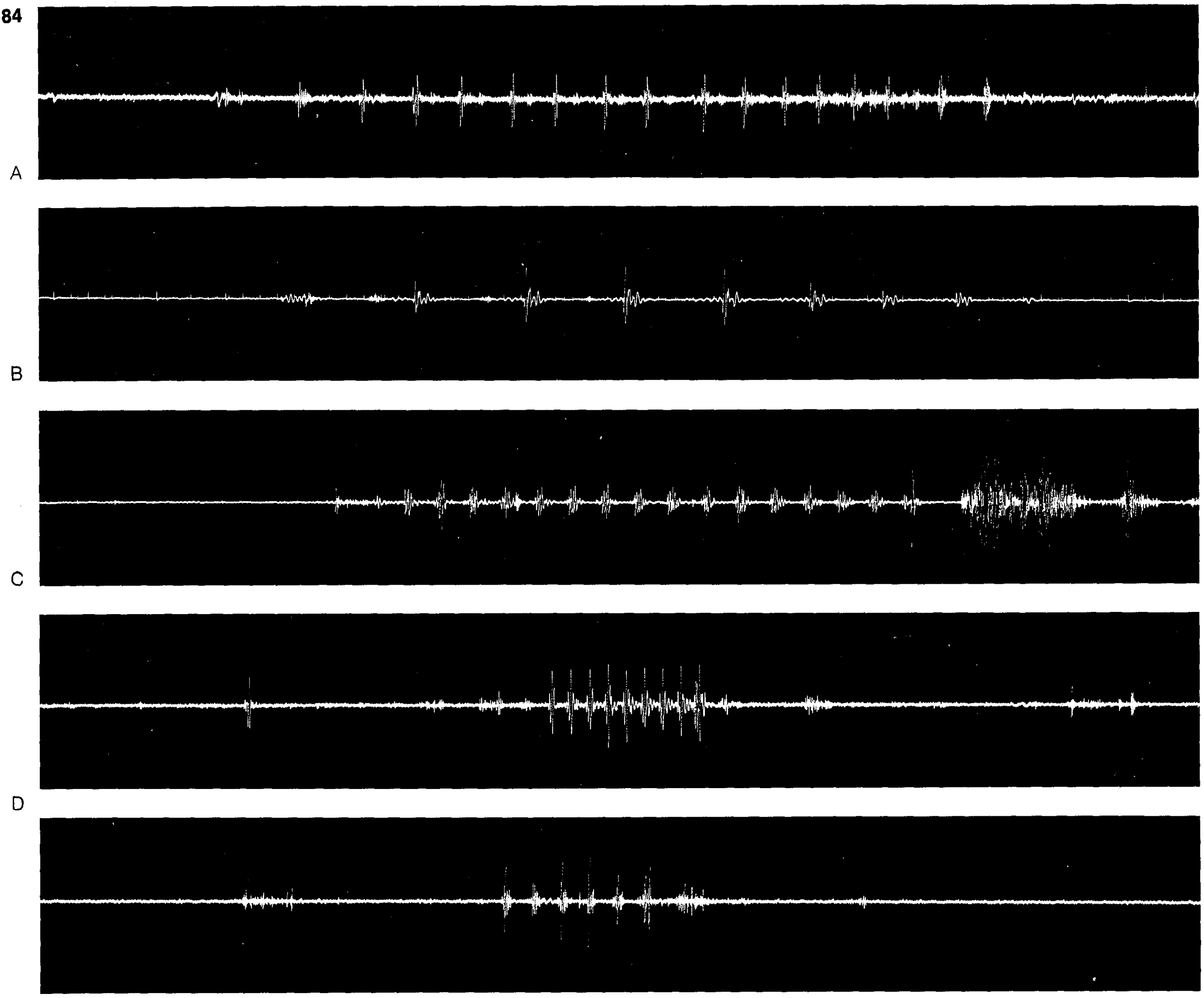
B. (*Amphiuca*) *chlorophthalmus crassipes*; outer claw. Data as in Pl. 15 *A-D*.

C. (*Deltuca*) *coarctata coarctata*; inner claw. Data as in Pl. 6 *E-H*.

D. (*Deltuca*) *coarctata coarctata*; outer claw. Data as in Pl. 7 *E-H*.

E. (*Australuca*) *seismella*; inner claw. Data as in Pl. 12 *A-D*.

F. (*Deltuca*) *demani typhoni*; data same as in Pl. 4 *E-H*.



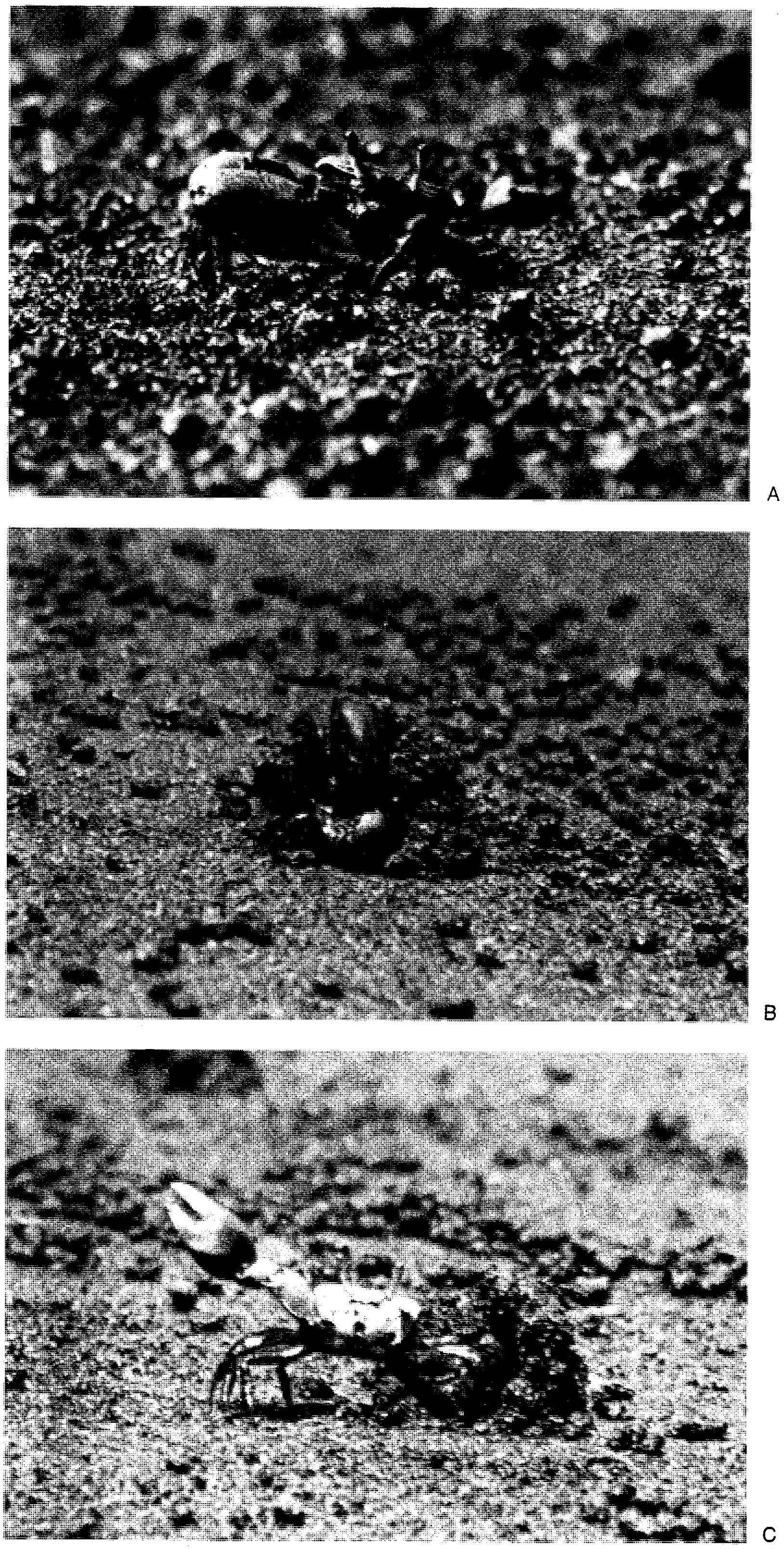
Pl. 47. Examples of sound production in *Uca*. All the sounds were made by burrow-holding males following the withdrawal of an intruding conspecific male. (P. 484.)

A. (*Thalassuca*) *vocans pacificensis*. Fiji Is. Time scale: 1 sec. = 12.5 cm.

B. (*Celuca*) *cumulanta*. Trinidad. Time scale: 1 sec. = 12.5 cm.

C. (*Celuca*) *lactea annulipes*. Red Sea. Time scale: 1 sec. = 12.5 cm.

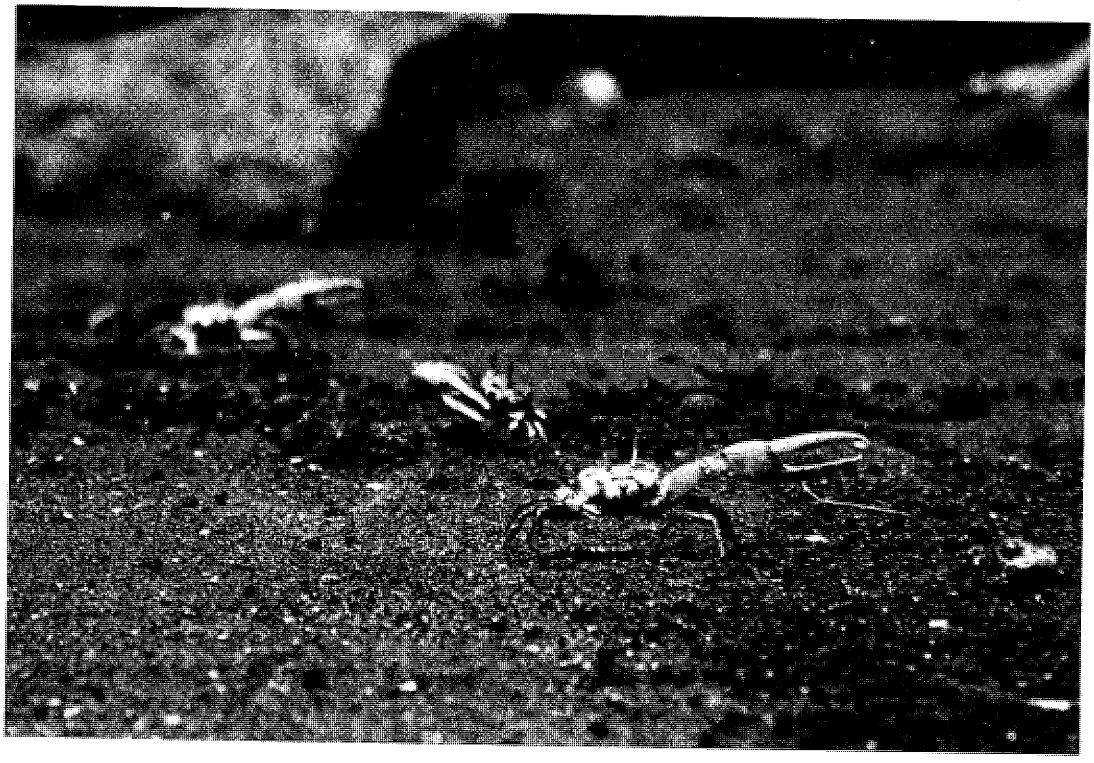
D. (*Celuca*) *lactea perplexa*. New Caledonia. Time scale: 1 sec. = 12.5 cm. The lower strip is a continuation of the upper.



Pl. 48. Activities by a single male, performed in sequence around his burrow. (*Celuca*) *latimanus*. Panama Canal Zone: Balboa. (P. 319.)

A. Feeding.
B. Building hood.
C. Waving display. The crab has now assumed display white.

Pl. 49. An example of hood construction at the peak of its development, both in relative size and in symmetry. Its builder is (*Celuca*) *musica terpsichores*; carapace lgth. ca. 7 mm. Panama Canal Zone: Balboa. (P. 500.)



PL. 50. Courtship in *Uca*. (P. 500.)

A. A group of males, chelipeds in rest position, face a wandering female as she crouches momentarily motionless. As soon as she started to walk again, the males resumed waving, turning as necessary to keep their anterior aspect directed toward her. (*Celuca*) *lactea annulipes*. Singapore.

B. Two males displaying toward a conspecific female, (*Celuca*) *stenodactylus*. The third male, facing to the left and not waving, is a member of a closely related species, (*Celuca*) *beebei*. Panama Canal Zone: Balboa.

Appendixes

Appendix A. Material Examined

It would be misleading, it seems, to list the total number of specimens of each species examined in the course of this study: the significance of the word *examined* changes from one species to the next. Sometimes, a great deal of time and effort was spent on a few specimens; in other cases, large numbers of individuals were examined, as in *lactea*, but the detailed work on most of these extended only to the gonopods and general claw shape, in order to establish subspecies and determine their ranges; only in series from selected localities did detailed study and comparison extend to many characters.

Comparison of the space consumed in the listing gives an idea of the totals, and in any individual case the numbers can be added up; general remarks on abundance or scarcity of a species in nature are usually included, when either attribute is noteworthy, in the introduction to each species.

Again, in most species the numbers of individuals observed in life far exceeded those I collected for later study or examined in other institutions. Even more than with the preserved material, of course, the detail with which living specimens were observed varied from species to species. An indication of my familiarity with each is given in the species treatments under the heading Field Material.

Probably the most useful function of this appendix is to show the present location of the material. The full names and addresses of the institutions abbreviated (USNM, BM, etc.) in the lists below appear on p. 678.

All of the specimens collected in the course of this study and formerly in the collections of the New York Zoological Society (NYZS) are now in the Smithsonian Institution, National Museum of Natural History, Washington (USNM). Type specimens included in that collection have already been assigned numbers by the museum and these are included here. Numbers for the rest of the specimens, indicated below simply by "(NYZS)," can be obtained directly from the museum: enough data are given in the listing to facilitate their selection there for future examinations; these numbers range approximately from 138043 to 138877. The great majority of the total number of preserved *Uca* in the world are deposited in the Smithsonian; even before the addition of the New York Zoological Society material the collection was by far the largest in existence; the total collection probably now numbers about 16,000 specimens, of which more than 14,000 have resulted from the present study.

Collections were also examined or material received on loan through the generous cooperation of other appropriate institutions in New York, Philadelphia, New Haven, Cambridge (Massachusetts), Los Angeles, London, Paris, Leiden, Amsterdam, Copenhagen, Göttingen, Frankfurt, Torino, Singapore, Port Moresby, Sydney, Yokohama, Fukuoka, and Honolulu. The Australian Museum in Sydney has a fine collection of *Uca* from Australia and neighboring shores. Unfortunately, when I stopped there briefly in 1956 I had not done sufficient taxonomic work on the group to profit by the material; it will reward future attention.

The subgenera, species, and subspecies are listed in the order given in the table of contents and the systematic section.

The authorities and references for all synonymized names included in these lists will be found in the systematic section, under the headings of Type Material and Nomenclature and of References and Synonymy. They also appear in the Index to Scientific Names (p. 719).

The order in which geographical names are listed is not always similar from one species to the next. In these exceptions the arrangements were selected because they seemed to be more helpful than strict consistency in making certain distributional comparisons among, for example, allopatric or sympatric forms. In no case was any attempt made to suggest palaeogeographic dispersal.

Geographical names are spelled in accordance with the form used on recent maps in English. In cases where another name or spelling is much more familiar than the currently accepted form, the older name is placed in brackets.

The abbreviations *G.* and *U.*, preceding species names in the listing of type-specimens examined, refer respectively to the generic names *Gelasimus* and *Uca.*

SUBGENUS *DELTUCA*

Uca (*Deltuca*) *acuta* (Stimpson, 1858). (P. 25.)

U. (*D.*) *acuta rhizophorae* Tweedie, 1950

MALAYSIA. *Sarawak*: Santobong (near mouth of river, below Kuching): HOLOTYPE of *U. rhizophorae*, m. (BM); 12 m., 2 f. (NYZS).

SINGAPORE. Geylang R. (near mouth): 4 m., 2 f. (NYZS). Jurong R. (near mouth): 1 m. (NYZS).

U. (*D.*) *acuta acuta* (Stimpson, 1858)

HONG KONG. Kowloon (Castle Peak area): NEOTYPE of *U. acuta*, m. (NYZS = USNM 137665); 37 m., 6 f. (NYZS).

CHINA. *Fukien*: Amoy: 4 m., 2 yg. f. (USNM 57033); 1 m. (USNM 125702); 2 m. (USNM 64953); 3 m. (USNM 64954); 1 yg. m., 1 yg. f. (USNM 74906); 1 m. (BM 2463 part). Tsimei: 2 m. (USNM 57812); 1 m. (USNM 57826). Chin B.: 1 m. (USNM 57055). Foochow: 2 m. (USNM 59096); 1 m. (USNM 59097). Guantoo (near Foochow): 1 m. (USNM 61845). Santu: 1 m. (USNM 61844); Kiaohsien [Kiaochow]: (BM; at least 2 m. = *a. acuta*). Liuwutien: 3 yg. m., 3 yg. f., ? 1 very yg. m., ? 1 very yg. f. (USNM 61843).

Uca (*Deltuca*) *rosea* (Tweedie, 1937). (P. 29.)

INDIA. Port Canning: 2 m., 1 f. (USNM 63673); 1 m., 1 f., + 7 yg. (USNM 63674). *Nicobar Is.*: Xancovri: 2 m., 1 f. (USNM 19711).

BURMA. Rangoon: 1 m. (MCZ 5787). *Mergui Archipelago*: 2 m. (Leiden reg. no. 4); 4 yg. (BM 86.52); 3 m. + yg. (Amsterdam: de Man collection).

MALAYSIA. *Malaya*: *Penang*: Penang: 95 m., 18 f. (NYZS). *Selangor*: Port Swettenham: HOLOTYPE of *G. roseus*, m. (BM); 2 m., 1 f. (NYZS; gift of M.W.F. Tweedie). *Negri Sembilan* (near Sungei Dua ferry): 29 m., 8 f., + 20 yg. (NYZS). *Malacca*: Malacca: 1 m. (USNM 19552).

INDONESIA. *Kalimantan* [*Borneo*]. Pontianak: 3 m., 1 f. (USNM 39162); 2 m. (Leiden 1535). *Sumatera* [*Sumatra*]. Atjeh: 1 yg. m., 1 yg. f. (USNM 39161).

Uca (*Deltuca*) *dussumieri* (Milne-Edwards, 1852). (P. 32.)

U. (*D.*) *dussumieri capricornis* subsp. nov.

AUSTRALIA. *Western Australia*: Broome: HOLOTYPE of *U. d. capricornis*, m. (NYZS = USNM 137675); 43 m., 30 f. (NYZS); Monte Bello Is.: 1 yg. m. (BM 1938.6. 13-1-2, part: lgth. 12 mm).

U. (*D.*) *dussumieri spinata* subsp. nov.

INDIA. Mouth of Hooghly R. (near Calcutta): 2 m. (BM 60.15).

BURMA. *Mergui Archipelago*: 1 m., 1 f. (Leiden 5); 1 yg. m. (Amsterdam); 1 m. (BM).

MALAYSIA. *Malaya*: *Penang*: 1 m. (Amsterdam). *Negri Sembilan*: near Sungei Dua: 1 m., 5 f. (NYZS). *Malacca*: Malacca: 1 m. (USNM 39174); 2 m. (Amsterdam). "Borneo." 1 m. (BM: Genard). *Sarawak*: Santobong (near mouth of river below Kuching): 4 m., 2 f. (NYZS; ex-Raffles, gift of M.W.F. Tweedie). *Labuan*: 2 m., 1 f. (Raffles). *Sabah* [N. Borneo]: Sebatic I.: 35 m., 35 f. (USNM 43428).

SINGAPORE. HOLOTYPE of *U. d. spinata*, m. (NYZS = USNM 137677); 24 m., 12 f. (NYZS); 3 m., 2 f. (Raffles).

INDONESIA. *Sumatera* [*Sumatra*]. Atjeh: 1 m. (USNM 39173). *Djawa* [*Java*]. 1 m. checked among 5 (Leiden 1242). Pasuruan (near Surabaja): 14 m., 1 f. (NYZS). Madoera: including 4 m. (Amsterdam); 2 m. (Leiden 2015). Zuidk (near Madoera): 1 m. (Leiden 2013). *Aru* [*Aroe*, *Arrou*] *Is.*: S. Manumbai: 4 m. (BM).

PHILIPPINE IS. *Palawan*: Nokoka Bay: 5 m. (USNM 43429).

THAILAND. Bangpoo (near Bangkok): 1 m. (USNM 94418); 1 f. (USNM 125708). Ajuthia: 2 m. (Paris). Lem Ngob: 1 f. (USNM 43296). Paknam: 2 m., 1 f. (USNM 63665); 2 m., 1 f. (USNM 63667.

CHINA. *Fukien*: Amoy: 1 m. (USNM 64959); 3 m. (Leiden 1244). Foochow: (Minhow): 2 m., 2 f. (USNM 61840); 1 m., 1 f. (USNM 58740); 2 m. (USNM 59091); 1 m. (USNM 59092). Liuwutien: 2 yg. m. (USNM 61841).

Locality Record Questionable. MADAGASCAR. Nossy Faly (on northwest coast): 1 m. (Leiden 1243 part). This is the specimen mentioned by de Man (1891: 26) as one of those figured by Hoffmann (1874: Pl. 3, Fig. 22); it is the only individual reported from the island according to Crosnier (1965). See page 35.

U. (*D.*) *dussumieri dussumieri* (Milne-Edwards, 1852)

INDONESIA. *Sumatera* [*Sumatra*]: Simeulue [Simaloer]: Sinabang [Sinaboung]: 10 m. checked in series (Leiden 2146). Nias: 3 m. (Amsterdam). Sibigo [Siboga]: 1 m. of series checked (Torino—see Nobili 1899). *Djawa* [*Java*]: 2 m. (BM 74.57). Samarang: LECTOTYPE of *G. dussumieri*, m. (Paris). Djakarta [Batavia]: 1 m. (Paris: Blecker); 1 m. (Paris: Blecker); 2 m. (Paris: Blecker). *Sulawesi* [*Celebes*]: Parepare: 2 m. (Amsterdam). *Adonara*: Sagoe: 2 yg. m. (Amsterdam). *Molucca Is.*: Batjan: 1 m. (BM). Ambon [Amboina]: 2 m. (Leiden 1245). *Aru* [*Aroe, Arrou*] *Is.*: 3 m. (Paris).

NEW GUINEA. *West Irian*: Japen: Seroei: Laut: 1 m. (Leiden). Mimika R.: 1 m. (BM). Hollandia Haven: 3 m. (Leiden). "Om geving Base," C. Hollandia: 2 m., 1 f. (Leiden: Holthuis collection 143). Territory of Papua and New Guinea: near Madang: 5 m., 4 f. (NYZS).

SOLOMON IS. 1 m. (Paris 1386).

AUSTRALIA. *Queensland*: Cooktown: 1 m. (Paris 4234); 1 m. (Paris 4239).

NEW CALEDONIA. 2 m. (Paris); 1 m. (Paris: A. le Comte). Near Nouméa: 5 m., 4 f. (NYZS).

CAROLINE IS. *Ponape*: 2 m. (Leiden 265). *Palau Islands*: 2 m., 2 f. (NYZS; collected by Takahasi, 1935; gift from T. Sakai, U. of Yokohama).

PHILIPPINE IS. *Sulu*: Tawi Tawi: 3 m., 1 f. (NYZS). Joló: 13 m., 18 f. (NYZS). *Mindanao*: Zamboanga: 3 m., 1 f. (USNM 43430); 113 m., 29 f. (NYZS). Gulf of Davao: Padada Beach: 1 f. (AMNH 8318). Davao (Agnow Swamp): 1 yg. f. (AMNH 8555 part). In and near mouth Padada R.: 1 yg. m., 2 yg. f. (AMNH 8393 part). Sasa: 1 f. (NYZS). Iling R., N. of Sasa: 10 m. (NYZS). Madaum: 1 yg. m., 3 yg. f., 1 mating pair (NYZS). *Negros Occ.*: 1 f. (USNM 25225). Magnanod R., Victorias, Bangi-Bangi: 1 m. (USNM 64981); 1 m. (USNM 64982); 2 f. (USNM 73273). *Lubang*: Looc: 2 m., 1 f. (USNM 43431). *Cebu*: Maston I.: 1 m. (USNM 43276). *Panay*: Jaro R.: 2 m., 2 f. (USNM 73184). Iloilo: 4 m., 1 f. (USNM 73201 part); 1 m. (USNM 125710); 1 f. (USNM 73221); 1 m. (USNM 73224); 1 f. (USNM 125703). "Shore around Iloilo R.": 1 m. (USNM 43433). *Guimares*: Jordan R.: 6 m., 2 f. (USNM 43432). *Samar*: Catbalogan: 1 m. (NYZS). *Palawan*: Puerto Princesa: 7 m., 7 f. (NYZS). Northwest coast, near mouth of Baheli R.: 6 m., 2 f. (NYZS). *Luzon*: Lamao: 1 m. (NYZS). Ragay Gulf: 7 m., 7 f. (USNM 43434).

NANSEI [RYUKYU or LOO CHOO] IS. *Ishiyaki I.*, mouth of Miyara R.: 1 m. (NYZS; collected by Ohishima, gift from T. Sakai, U. of Yokohama).

Additional Material with Incomplete or Questionable Locality Records.

SOUTHERN PACIFIC. (USNM 17764.)

TUAMOTU ARCH.: Toan Atoll: 1 m. (USNM 93283 part). *Locality doubtless in error*; see p. 41.

Uca (*Deltuca*) *demani* Ortmann, 1897. (P. 39.)

U. (*D.*) *demani australiae* subsp. nov.

AUSTRALIA. *Western Australia.* Broome: HOLOTYPE of *U. d. australiae*, m. (USNM 64250).

U. (*D.*) *demani typhoni* subsp. nov.

PHILIPPINE IS. *Negros Occ.*: 1 m. (USNM 25223); 1 m. (USNM 65012). *Panay*: Iloilo 1 m., 1 f. (USNM 73163 part); 16 m., 6 f. (USNM 73201 part); 3 yg. m., 2 yg. f. (USNM 73211 part); 4 m., 1 yg. m. identity?, 2 yg. f. (USNM 73221 part). Jaro R.: 1 m. (USNM 73222 part). *Lubang*: Looc: 1 m., 2 yg. f. (USNM 43437 part). Basus R.: 1 yg. f. (USNM 43435). *Samar*: Catbalogan: 1 m., 1 f. (NYZS). *Luzon*: Manila: HOLOTYPE of *U. d. typhoni*, m. (USNM 43041).

TUAMOTU ARCH.: Toan Atoll: 2 m., 1 f. (USNM 93283 part). *Locality doubtless in error*; see p. 41.

U. (*D.*) *demani demani* Ortmann, 1897

INDONESIA. *Djawa* [*Java*]. Pasuruan (near Surabaja): 1 m. (Amsterdam, one examined of several labeled *demani*). *Sumbawa*: Baii van Bima: 1 m. (Amsterdam; de Man's 2nd specimen, referred to *forcipata*, 1892.1, included in Ortmann's proposal of the new name, 1897). *Sulawesi* [*Celebes*]: LECTOTYPE of *G. demani*, m. (Leiden 1257; de Man's first specimen, 1891.3:32).

PHILIPPINE IS. *Mindanao*: Zamboanga: 6 m. (USNM 43307: Type series, including type, of *Uca zambo-*

angana); 53 m., 6 f. (NYZS). Gulf of Davao: Padada Beach: 16 m., 14 f., most of them yg. (AMNH 8304, 8306 part, 8307, 8308 part, 8310, 8313, 8330, 8331, 8332, 8380 part). In and near mouth Padada R.: 8 m., 15 f., most of them yg. (AMNH 8342, 8343, 8386, 8387, 8388, 8390, 8391 part, 8392, 8393 part). Malalag: 3 m. (NYZS). Davao Beach: 3 m., 2 f. (AMNH 8421, 8422, 8554). Sasa: 1 m. (NYZS). Iling R., N. of Sasa: 2 m. (NYZS).

Uca (Deltuca) arcuata (de Haan, 1835). (P. 44.)

NORTH VIETNAM. *Tonkin*: Pointe du Scorpion ("brought by a fisherman"). 1 m. (Paris 1028).

HONG KONG. 1 m., 2 f. (BM 1935.3.19); Kowloon (Castle Peak area): 5 m. (NYZS).

CHINA. "Chine": Type material of *G. brevipes* (Paris). *Fukien*: Amoy: 1 m. (BM 2463); 2 m., 1 f. (USNM 57813). Foochow: 1 f. (USNM 57613); 1 f. (USNM 59093); 1 m. (USNM 59094); 1 m. (USNM 59095); 1 m. (USNM 61847); 1 m., 1 f. (USNM 61849); 3 m., 1 f. (USNM 63709); 1 m., 1 f. (USNM 75441). Guantoo (near Foochow): 1 m. (USNM 61848). Muiwha (near Foochow): 1 m., 3 f. (USNM 61842). Santuao 2 m., 2 f. (USNM 61850). *Chekiang*: Wenchow: 2 m., 4 f. (USNM 74604); Liuwutien: 1 yg. f. (USNM 61846).

TAIWAN [FORMOSA]. Takao: Shenshoshi: 3 m. (USNM 55424). Ampin: 1 m. (USNM 57492). Taichu: Soroku: 1 f. (USNM 55398). Shinchika: 1 f. (USNM 55400). Toutti: 2 m., 1 f. (BM 84.10). Tamsui: 158 m., 4 yg. m., 1 yg. f. (NYZS). Taihoku: 1 m. (USNM 55399).

KOREA [CHOSEN]. 2 m., 1 f. (USNM 19708); yg. (BM 92-12-15-1-7).

JAPAN. LECTOTYPE of *G. arcuatus*, m., + 3 m., 1 f., labeled "*Gelasimus arcuatus* de Hn. Types" (Leiden 243) + series (Leiden 244, 245); 1 m. (USNM 17762). *Kyushu*: Ariake Bay: 1 f. (NYZS).

Uca (Deltuca) forcipata (Adams & White, 1848). (P. 48.)

MALAYSIA. *Malaya. Penang*: 10 m., 1 f. (NYZS); 1 f. (USNM 39163); 1 yg. m., 1 yg. f. (USNM 43306); 1 m. (Paris). *Negri Sembilan*: Sungei Dua: 11 m., 13 f. (NYZS). "Borneo." HOLOTYPE of *G. forcipatus*, m. (BM "Borneo 44.106; 4476"). *Sarawak*: Kuching: 1 m. (Torino). *Sabah* [N. Borneo]: Sebatic I.: 1 m. (USNM 125705); 1 m., 3 f. (USNM 43438; note inside vial says "m. compared by Calman with type of *forcipata*").

SINGAPORE. 4 m. (NYZS): 3 m. (NYZS; ex-Raffles, gift of M.W.F. Tweedie).

INDONESIA. *Kalimantan* [*Borneo*]. Samarinda: 1 m. (Torino). *Sumatera* [*Sumatra*]. Buttikofer: 2 m. (Leiden 2033). *Djawa* [*Java*]: near Surabaja: swamp at Trengglunga: 79 m., 2 f. (NYZS). *Near Surabaja*: swamp at Paseruan: 12 m. (NYZS). *Sulawesi* [*Celebes*]. Makassar: 2 m., 1 f. (MCZ 7255).

PHILIPPINE IS. *Mindanao*: Zamboanga: 1 m. (BM 84.31. HMS *Challenger*. Locality record questionable, since designated depth ["10 faths."] impossible. Name on label: *rubripes*. *Samar*: Silaga R.: 2 m., 2 f. (USNM 43436). *Negros Occ.*: Magnanod R., Victorias: 1 m. (USNM 73269). Bangi-Bangi: 2 m. (USNM 64991); 1 m. (USNM 73271); 3 yg. m. (USNM 73221 part). West coast of *Palawan*: Baheli R. 9 m., 4 f. (NYZS). *Palawan*: Puerto Princesa: 4 yg. m., 1 yg. f. (NYZS).

THAILAND. Bangpoo (near Bangkok): 3 m., 1 f. (USNM 94419). Paknam: 2 yg. m., 3 yg. f. (USNM 125706); 1 m. (USNM 63666). Lem Ngob: 6 m., 2 f. from type material of *U. manii* Rathbun (Copenhagen); 4 m. from same series, including one compared by Calman with type of *G. forcipatus* (USNM 39714).

TUAMOTU ARCH. Toan Atoll: 1 m., 1 f. (USNM 93283 part). *Locality doubtless in error*; see p. 41.

Uca (Deltuca) coarctata (Milne-Edwards, 1852). (P. 52.)

U. (D.) coarctata coarctata (Milne-Edwards, 1852)

[RUSSIA.] "Odessa": LECTOTYPE of *G. coarctatus*, m. (Paris). *Locality name unquestionably erroneous*; ? 1 f. same locality, separate box, poor condition.

INDONESIA. *Sumatera* [*Sumatra*]: Simeulue [Simaloe] I.: 3 m., 3 f. (NYZS; ex-Raffles, gift of M.W.F. Tweedie). Nias: series (Amsterdam). Benkulen: 6 m., 2 f. (USNM 75865). *Djawa* [*Java*]: 1 m. (BM 74.57). Djakarta: (Paris). *Sulawesi* [*Celebes*]: Togian I.: 1 m. (USNM 19556). *Seram* [*W. Ceram*]: Piroe: yg. (Amsterdam). *Aru* [*Aroe, Arrou*] *Is.*: Manumbai: 3 m. (BM 1935.1.28.1-3).

NEW GUINEA. *West Irian*: Noord [Lorentz] River: 2 yg. m. (Amsterdam). Mimika R. near Kokonau: 1 m. (BM 1911.8.1.25). Near Hollandia: 1 m. (Leiden). Territory of Papua and New Guinea: 3 m., 4 f. (NYZS).

AUSTRALIA. *Queensland*: Cooktown 1 m. (Paris 2089). Cairns: 12 m., 3 f. (MCZ 5786); 1 m. (USNM 22198). Gladstone: 5 m. (NYZS); 1 m. (Paris 1981).

NEW CALEDONIA. 2 m. (Paris, M. Balansa); series, poor condition (A. Milne-Edwards). Near Nouméa: 9 m., 3 f. (NYZS).

FIJI IS. *Viti Levu*: Suva: paratype of *U. ischnodactylus*, 1 m. (USNM 99261). 5 m., 4 f. (NYZS). Near mouth of Wainibokasi R., near Rewa: 5 m. (NYZS). Raki-Raki: 9 m., 3 f. (NYZS). Tavua: 53 m., 13 f. (NYZS). Lautoka: 5 m., 3 f. (NYZS).

? TAHITI. 1 m. (USNM 19662). *Locality error probable.*

PHILIPPINE IS. *Mindanao*: Zamboanga: 24 m., 3 f. (NYZS). Gulf of Davao: Padada Beach: 1 yg. f. (AMNH 8306 part); 1 f. (AMNH 8338); 1 m. (AMNH 8339); 3 f. (AMNH 8377); 1 yg. m., 1 yg. f. (AMNH 8378); 2 yg. m. (AMNH 8379); 7 m., 3 f. (AMNH 8380 part). In and near mouth of Padada River: 1 yg. f. (AMNH 8344); 1 m. (AMNH 8394). Davao Beach: 2 yg. m. (AMNH 8308 part). Davao: Agdow Swamp: 3 yg. m. (AMNH 8555 part); ? 1 f. (USNM 43383; type of *U. mearnsi*). Madaum: 1 m., 1 yg. f. (NYZS). Iling R. (N. of Sasa): 2 m. (NYZS). *Panay*: Jaro R.: 1 m. (USNM 125707); 1 m. (USNM 73225 part). Iloilo: 1 m. (USNM 125709). *Samar*: Catbalogan: 1 m. (NYZS). *Luzon*: Bataan (Samal): 1 m. + drawn gonopod (body missing) (NYZS). Manila: 2 m. (BM 72.7). Dagadagatan R.: Navotas (near Manila): 1 m. (NYZS). Manila: 2 m. (USNM 43040; labeled *U. rathbunae* Pearse; collected and identified by him; see p. 55).

U. (*D.*) *coarctata flammula* subsp. nov.

NEW GUINEA. *West Irian*: Boshek near Biak: series (Leiden). Japen I.: Seroei: 1 yg. (Leiden). Merauke: series (Amsterdam). Merauke (near Kampong Sawa): 1 yg. m. (Leiden).

AUSTRALIA. *Northern Territory*: Darwin: HOLOTYPE of *U. c. flammula*, m. (NYZS = USNM 137676); + 20 m., 4 f. (NYZS). *Western Australia*: Broome: 2 m., 2 f. (USNM 56419); 2 m., 1 f. (USNM 56420); 25 m., 17 f. (NYZS). Port Walcott (near Dampier Archipelago): 1 m. (BM 89.5.12.2). Nicol B.: 2 m. (BM 69.38). Monte Bello Is.: 1 m. (USNM 46348); 1 m. (BM 1938.6.13.1.2). Mermaid Strait: 1 m. (USNM 19550).

Uca (*Deltuca*) *urvillei* (Milne-Edwards, 1852). (P. 58.)

[NEW HEBRIDES.] "*Vanikoro*": LECTOTYPE of *G. urvillei*, m. (Paris). *Locality name unquestionably erroneous.*

INDIA. *Malabar*: 1 m. (Paris). This specimen is one of 2 m. labeled "Type" of *G. dussumieri* Milne-Edwards.

PAKISTAN. Karachi: 1 m. (BM 97.9.12.1); 1 m. (BM 82.3).

EAST AFRICA. *Tanzania. Pemba Island*: Kiburunzi (near Chake Chake): 36 m., 19 f. (NYZS). *Zanzibar*: 3 lots of dried specimens (Paris). *Zanzibar* (near Muongoni): 3 m., 1 f. (NYZS). *Tanga*: Dar es Salaam (near Mtoni): 2 m. (NYZS).

MADAGASCAR. 2 m. (Leiden 1243); (Paris, several series, including 266, 339, and 130.96).

SOUTH AFRICA. Durban: 1 m. (Amsterdam 1894).

SUBGENUS *AUSTRALUCA*

Uca (*Australuca*) *bellator* (Adams & White, 1848). (P. 64.)

Uca (*A.*) *bellator bellator* (Adams & White, 1848)

INDIA. *Nicobar Is.*: Nankauri: 1 m. (USNM 22286).

MALAYSIA. *Labuan*: 2 m. (NYZS; gift of Raffles); 6 m., 4 (1 ovig.) f. (NYZS; gift of Raffles).

INDONESIA. *Djawa* [*Java*]: "Java": small series (BM 74.51). Djakarta [Batavia]: small series (Leiden 1255); 1 m., which is apparently part of type material of *G. signatus* var. *angustifrons* (Leiden 1536); series (Leiden 2016). Near Tilliwong (northwest coast): 1 m. (Leiden 2017). Bahduheira: small series (Leiden 2662). Semarang: 83 m. with claws, 102 m. bodies, many detached claws, 72 (25 ovig.) f. (NYZS). Madoera: 1 m. (Leiden 2037). Near Surabaja (at Trengglunga): 1 m. (NYZS).

NEW GUINEA. *West Irian*: Merauke: 1 m. (Torino); near Merauke: 3 m. (Leiden).

PHILIPPINE IS. "*Philippines*": HOLOTYPE of *G. bellator*, m. (BM). *Mindanao*: Zamboanga: 1 m. (NYZS). Gulf of Davao: Iling R. (north of Sasa): 1 m. (NYZS); Madaum: 4 m. (NYZS). *Negros Occ.*: Magnanod R. (near Victorias at Bangi-Bangi): 1 f. (USNM 65009). *Panay*: Jaro R.: 1 m. (ex-USNM 73225). *Palawan*: Puerto Princesa: 1 f. (NYZS). *Luzon*: Dagadagatan R. (near Manila, above Navotas): 11 m., 4 f. (NYZS).

U. (*A.*) *bellator signata* (Hess, 1865)

AUSTRALIA. "Australia": TYPE-SPECIMEN of *G. signatus*, m. (Göttingen 3665, in 53b). "*East Coast Australia*": 2 m. (Leiden 1261). *Queensland*: Port Curtis: 14 m. & f. (BM 8131). Gladstone: 6 m., 4 f. (NYZS). Boyne R. (above Gladstone): 4 m., 2 f. (NYZS).

U. (*A.*) *bellator longidigita* (Kingsley, 1880)

AUSTRALIA. *Queensland*: seaward from Brisbane: S. bank of Brisbane R., near mouth, Sandgate, and Shorncliffe: 22 m., 6 (5 ovig.) f. (NYZS).

U. (*A.*) *bellator minima* subsp. nov.

AUSTRALIA. *Northern Territory*: near Darwin: Ludmilla Creek, near junction with Golf Club R.: HOLOTYPE m. (NYZS = USNM 137668) + 5 m., 7 f. (NYZS).

Uca (*Australuca*) *seismella* sp. nov. (P. 70.)

AUSTRALIA. *Western Australia*: Broome: 2 yg. m. (NYZS). *Northern Territory*: near Darwin: Golf Club R.: HOLOTYPE m. (NYZS = USNM 137666) + 29 m., 2 ovig. f. (NYZS). *Queensland*: Gladstone: 7 m., 4 (1 ovig.) f. (NYZS).

Uca (*Australuca*) *polita* sp. nov. (P. 72.)

AUSTRALIA. *Western Australia*: Nicol B.: 4 specimens (BM 69-38). Broome: 13 m., 11 f. (NYZS). *Queensland*: Gladstone: HOLOTYPE m. (NYZS = USNM 137667) + 7 m., 4 (ovig.) f. (NYZS). *Thursday I.*: 2 m. (NYZS: gift; donor unknown).

SUBGENUS *THALASSUCA*

Uca (*Thalassuca*) *tetragonon* (Herbst, 1790). (P. 77.)

EGYPT. "EGYPTE": NEOTYPE of *U. tetragonon*, m. (Paris) + 1 f. (Paris: both marked "Type" by A. Milne-Edwards).

ETHIOPIA. *Eritrea*: 1 m. (Torino 1763). Near Bosso: 1 m. (Torino 2276). Isole Key: 1 m. (Torino 2072). Massawa: 2 m., 1 f. (AMNH 4323 part); 23 m., 3 f. (NYZS); 2 m. (Torino 665 & 2098). Near Massawa: Green I.: 39 m., 24 f. (NYZS).

ADEN. 1 m. (USNM 19324).

EAST AFRICA. *Tanzania*: *Zanzibar*: between Chakwani and Mbeni, Kombeni B. and Chwaka: 52 m., 10 f. (NYZS).

INDIAN OCEAN. *Aldabra I.*: 1 m. (USNM 17749). *Mauritius*: 2 m., 1 f. (USNM 19654); 1 m., 3 f. (Philadelphia 2932: labeled *G. desjardinii* Guérin). *Chagos Is.*: Diego Garcia: 1 m. (BM 1910.4.30.18).

BURMA. Rangoon: 1 m. (MCZ 5779 part).

PHILIPPINE IS. *Sulu*: Tawi Tawi: 2 m., 2 f. (NYZS). *Mindanao*: Gulf of Davao: Padada Beach: 1 yg. m. (AMNH 8367).

NEW GUINEA. 1 m. (Torino). *West Irian*: Japen I., near Seroei: small series (Leiden: Holthuis collection, 25 Feb. 1955). Noemfoor: 2 m. (Leiden: Leg. Hendriksen, 1953). New Hollandia: 1 m. (Leiden: Leg. Van Hout, 1955). Reef at Marine Kazerne: 2 + ? 1 yg. m. (Leiden 683).

AUSTRALIA. Sydney: Type material of *G. variatus*, 2 m. (Göttingen 52a; *exact locality questionable*; see p. 80). "Australien": Type material of *G. variatus*, 1 m. (Göttingen 52b).

NEW CALEDONIA. 1 m., 1 f. (Paris: both marked "Type" of *G. tetragonon* by A. Milne-Edwards).

PACIFIC OCEAN. *Caroline Is.*: small series (BM 98.11.1.1-5 part). *Wake I.*: Series (Bishop). *Marshall Is.*: Jaluit, Marchalsoerne: 1 m., 1 f. (USNM 19709). *Gilbert Is.*: Apiang: 2 m., 2 (1 ovig.) f. (USNM 93282). *Ki Is.*: 1 m. (BM 1910.3.29.18). *Samoa*: Savaii I.: 1 m. (BM 74.54). Apia: 9 m., 10 f. (NYZS). *Friendly Is.*: Tonga: Tongatabu: 5 m. (USNM 33164). *Line Is.*: Fanning I.: Inner lagoon:

1 f. (USNM 46682). Penrhyn I.: 8 m. (AMNH 7454); 1 f. (AMNH 7476); 1 m. (AMNH 7477). *Society Is.*: Bora-Bora: 21 m., 18 f. (NYZS). Raiatea: 2 m., 1 f. (NYZS). Tahiti: 1 f. (MCZ 5806); (at Faaa): 16 m., 14 f. (NYZS). *Tuamotu Is.*: Raroia Atoll (S. end of Oneroa I.): 31 m. and f. (USNM 94558).

? *Hawaii.* "Isles Sandwich": 1 m., 1 f. (Paris: both marked "Type" of *G. tetragonon* by A. Milne-Edwards). *Locality questionable*; "Iles Sandwich" perhaps an error for Bora Bora; see pp. 80 and 324.

Not Examined. About 50 additional specimens at USNM from localities from which other representatives are included in the material listed above.

Uca (Thalassuca) formosensis Rathbun, 1921. (P. 83.)

TAIWAN [FORMOSA]. *Taichu*: Rokko: TYPE SERIES of *U. formosensis*, 2 m. (USNM 54472); 1 f. (USNM 55385). Tamsui: 2 m., 1 f. (NYZS; gift of T. Sakai, U. of Yokohama). Giran (northeast coast): 1 m. (USNM 55386).

Uca (Thalassuca) vocans (Linnaeus, 1758). (P. 85.)

For additional specimens examined, but not referred to subspecies, see note at end of listing for the species, below (p. 598).

U. (T.) vocans borealis subsp. nov.

HONG KONG. HOLOTYPE of *U. vocans borealis*, m., (NYZS = USNM 137669) + 80 m., 84 f. (NYZS); 1 m. (USNM 44358).

CHINA. *Fukien*: Chin Bey (near Amoy): 1 ovig. f. (USNM 57051). Tsimei: 2 ovig. f. (USNM 57825); 3 m., 2 (1 ovig.) f. (USNM 57826).

TAIWAN [FORMOSA]. Tamsui: 3 m. (NYZS).

U. (T.) vocans pacificensis subsp. nov.

INDONESIA. *Ambon* [*Amboina*]: 2 m. (Leiden D 275).

PHILIPPINE IS. (probably hybridizing with *U. vocans vocans*). *Sulu*: Tawi Tawi: 26 m., 11 f. (NYZS). Joló: 1 m., 2 f. (NYZS); Princess Tarhata Kiram's Beach): 3 m., 2 ovig. f. (NYZS). *Mindanao*: Zamboanga: 16 m., 8 f. (NYZS). Gulf of Davao: Padada Beach: 1 m. (AMNH 8362); 1 m. (AMNH 8401 part). Madaum: 1 m. (NYZS).

NEW GUINEA. *Territory of Papua and New Guinea* (probably hybridizing with *U. vocans vomeris*): Near Madang on north central coast: Maiwara: 4 m., 1 f. (NYZS). Port Moresby: Taurama Beach and Bootless B.: 2 lots: 3 m. (UPNG; collected by M. Cahill).

PACIFIC OCEAN. *Marshall Is.*: 3 m. (MCZ 5773). *Guam*: 12 m., 2 f. (Bishop). *Fiji Is.*: *Viti Levu*: Suva: HOLOTYPE of *U. vocans pacificensis*, m. (NYZS = USNM 137670) + 28 m., 14 f. (NYZS). Rewa (flats at mouth of Wainibokasi R.): 18 m., 22 f. (NYZS). *Samoa Is.*: 15 m. (NYZS); 1 m., 1 f. (Leiden 2665).

U. (T.) vocans dampieri subsp. nov.

AUSTRALIA. *Northern Territory*: Darwin: 28 m., 19 f. (NYZS). *Western Australia*: Broome: HOLOTYPE of *U. vocans dampieri*, m. (NYZS = USNM 137671) + 33 m., 40 f. (NYZS).

U. (T.) vocans vomeris McNeill, 1920

NEW GUINEA. *Territory of Papua and New Guinea*: near Madang on north central coast: Maiwara: 13 m., 16 f. (NYZS). Port Moresby: Fisherman's I.: 1 m. (UPNG; collected by M. Cahill).

NEW CALEDONIA. Near Nouméa: mouth of Dumbea R.: 6 m. (NYZS).

AUSTRALIA. *Queensland*: Shorncliffe (near mouth of Brisbane R.): 1 m. (NYZS). Sandgate (near mouth of Brisbane R.): 2 m. (AMNH 4884). *New South Wales*: Trial B.: 2 m., 2 f. (now in poor condition; Bishop 601); 3 m., 2 f. (Bishop 2482).

U. (T.) vocans hesperiae subsp. nov.

ETHIOPIA. *Eritrea*: Massawa: 17 m., 6 f. (NYZS).

EAST AFRICA. TANZANIA. *Pemba I.*: Chake Chake: 2 m. (NYZS). Zanzibar: Chakwani Fish Ponds:

HOLOTYPE of *U. v. hesperiae*, m. (NYZS = USNM 137672) + 4 m., 10 f. (NYZS): between Chakwani and Mbeni: 17 m., 6 f. (NYZS).

MADAGASCAR. Eau Saumâtre: 1 f. (Paris). Nossy Bé: 9 m. (Leiden D 274, labeled *marionis excisa*; see p. 89).

CEYLON. *Negombo* (near Colombo): 1 m. (NYZS).

MALAYSIA. *Malaya*: Penang (probably hybridizing with *U. vocans vocans*): 1 m. (NYZS).

SINGAPORE. (Probably hybridizing with *U. vocans vocans*): 1 m. (NYZS; gift of M.W.F. Tweedie).

INDONESIA. *Sulawesi* [*Celebes*]: Padang. 1 m. (Leiden 2751).

U. (T.) vocans vocans (Linnaeus, 1758)

BURMA. Rangoon: 9 f. (MCZ 5779 part).

MALAYSIA. *Malaya*: Penang: 1 m. (NYZS). Port Dickson: 2 m., 1 f. (Leiden 5269). *Borneo*: *Sabah* [*N. Borneo*]: Labuan: 1 m., 1 f. (NYZS; gift of M.W.F. Tweedie).

SINGAPORE. 6 m. (NYZS; gift of M.W.F. Tweedie). Geylang R. (near mouth): Kallong: 21 m., 29 f., + 1 copulating pair (NYZS).

INDONESIA. *Bawean*: Sangapura: 30 m., 3 f. (NYZS; gift of H. Oesman). *Djawa* [*Java*]: Tanjong Priok (near Djakarta): 1 m. (Leiden 1491). North coast: 4 m. (Leiden 2048). Trengglunga (near Surabaja): 9 m., 3 f. (NYZS). Pasuruan (near Surabaja): 8 m., 18 f. (NYZS); Besoeki: 6 m. (Leiden 277, 1674); Madoera; 4 m. (Leiden 2045). *Sulawesi* [*Celebes*]: Makassar: 1 m. (Leiden 5268). *Halmahera*: Ternate: 1 m. (Leiden 1533).

PHILIPPINE IS. *Sulu*: Tawi Tawi: 5 m., 3 ovig. f. (NYZS). Joló: 2 m., 2 f. (NYZS); Princess Tarhata Kiram's Beach: 3 m. (NYZS). *Mirdanao*: Zamboanga: 117 m., 38 f. (NYZS). Gulf of Davao: Padada Beach: 1 f. (AMNH 8325); near mouth of Padada R.: 3 m. (AMNH 8401 part); flats about 2 miles south of Padada: 2 m. (AMNH 8556). Sasa: 1 f. (NYZS). Madaum: NEOTYPE of *U. vocans*, m. (NYZS = USNM 137673) + 33 m., 16 f. (NYZS). *Palawan*: Puerto Princesa: 36 m., 21 f. (NYZS). Northwest coast, near mouth of Baheli R.: 8 m., 2 f. (NYZS). *Luzon*: Lamao: 1 m. (NYZS).

NANSEI [RYŪKYU or LOO CHOO] IS. 1 m. (MCZ 1333). Ishiyaki I. (mouth of Miyara R.): 3 m. in 2 lots. Kume-jima: 3 m. (NYZS; collected by Minei, gift of T. Sakai, U. of Yokohama).

Additional Material of Uca vocans Examined Sufficiently for Species Identification, but not Referred to Subspecies. At the time of visits to several European institutions made during the first years of this taxonomic revision, I had not yet distinguished the characteristics upon which the subspecies have since been based. Although for the most part, as with any African specimens, the subspecies can be safely presumed from the locality, individuals from Indonesia, New Guinea, and the Philippines may be from mixed populations. They are all therefore listed here only under the name of the species, *U. vocans*.

RED SEA. 1 m. (Leiden 1493).

MADAGASCAR. Nossy Bé. Short series (Leiden 275; labeled, as are the 9 m. already listed under *U. v. hesperiae*, Leiden 274, "*U. marionis excisa*," see p. 89).

NEW GUINEA. *West Irian*: A long series from Kotabaru [Hollandia], Japen and their vicinity (Leiden, several lots, collected by Holthuis, 1954ff.; specimens not examined individually).

PHILIPPINE IS. Holotype of *G. cultrimanus*, 1 m. (BM 43.6 Cuming collection).

CAROLINE IS. 1 m. British Museum.

Uca vocans: *Specimens not Examined.* More than 1,000 specimens at USNM from a variety of localities throughout the range of the species. The longest series, totaling 727 m. + 140 f., is from Iloilo, Panay I., in the Philippines and would form an excellent basis for future work on variations and the possible hybridization of subspecies (USNM 73164). Other outstanding series are 42 m. from Benkulen, Sumatra (USNM 75873) and 33 m. + 5 f. from Apia, Samoa (USNM 43300). This collection is currently labeled and catalogued under the following names: *U. cultrimana, marionis, marionis* var. *nitidus*, and *marionis vomeris*.

SUBGENUS *AMPHIUCA*

Uca (Amphiuca) chlorophthalmus (Milne-Edwards, 1837). (P. 98.)

U. (A.) chlorophthalmus crassipes (Adams & White, 1848)

INDIA. Car Nicobar: 3 m., 1 f. (NYZS; gift of Raffles Museum, Singapore).

INDIAN OCEAN. Cocos or Keeling Is.: 6 m., 3 f. (NYZS; gift of Raffles, Singapore).

MALAYSIA. *Malaya*: *Penang*: 1 f. (USNM 43370).

HONG KONG. 2 m. (USNM 43849); Kowloon (Castle Peak area, east of mouth of Deep Bay): 2 m. (NYZS).

JAPAN. *Tokaito coast*: Oho Sima: 2 f. (USNM 22288).

NANSEI [RYUKYU or LOO CHOO] IS. Kume-jima: 1 m. (USNM 73258); carapace only (USNM 73259).

PHILIPPINE IS. "Sinquejor": LECTOTYPE of *G. crassipes* (BM 902 43b). *Sulu*: Tawi Tawi: 3 m. (NYZS); Tapiantana I.: 1 m. (USNM 43451). *Mindanao*: Zamboanga: 1 f. (USNM 43371); 72 m., 47 (18 ovig.) f. (NYZS).

INDONESIA. *Molucca Is.*: Bourou I.: 1 m. (Phil. Acad.). *Aru* [*Aroe*, *Arrou*] *Is.*: 8 m., 1 f. (Paris).

NEW GUINEA. "New Guinea": type series of *U. novaeguineae*, 2 m. (USNM 6374). *West Irian*: in and near Kotabaru [Hollandia], Noemboor, and Biak: numerous m. & f. (Leiden 635 [part], 714, 723, 743 [part], and unnumbered; collected by Holthuis, 1954-1955; samples only examined in detail by Crane). *Territory Papua and New Guinea*: near Madang on north central coast: Maiwara: 6 m., 4 (1 ovig.) f. (NYZS). Port Moresby: 10 m., 2 f. (UPNG; collected by M. Cahill); Bootless B.: 4 m., 2 f. (UPNG; collected by M. Cahill).

PACIFIC OCEAN. *Caroline Is.*: Kusaie: 1 m. (USNM 33167); 4 m., 1 f. (MCZ 8845); Strong I.: 7 m., 3 f. (MCZ 5792); Ponape [Ascension]: 1 f. (MCZ 5967). *Marshall Is.*: 2 m., 2 f. (USNM 81379); 15 m., 18 f. (MCZ 5790); Ebon: 6 m., 1 f. (MCZ 5791). *New Hebrides*: Port Resolution: 2 m. (Paris, from Australian Museum). *New Caledonia*: short series (Paris). Balansa: 1 m., 1 f. (USNM 20299). Nouméa: 1 m. (NYZS). *Fiji Is.* [*Viti*]: 1. (Paris). *Viti Levu*: Suva: 2 (1 ovig.) f. (NYZS). *Samoa Is.*: Upolu: Apia: 3 m. (Torino); 12 m., 4 (3 ovig.) f. (NYZS). *Friendly Is.*: Tongatabu: "type non specifié" of *G. gaimardi*, m. (Paris). *Society Is.*: Bora-Bora: "type non specifié" of *G. latreillei*, 1 m. (Paris); 22 m., 9 f. (NYZS). Raiatea: 12 m. (AMNH 2482); 4 m. (NYZS). Tahiti: small series (Paris); Faaa: 79 m., 69 (5 ovig.) f. (NYZS). *Marquesas Is.*: 1 m. (USNM 81415 part). ["Iles Sandwich": 2 m. (Paris). Perhaps an error for Bora Bora; see p. 324].

Note. The material in Paris was originally labeled variously *chlorophthalmus*, *gaimardi*, *latreillei*, and *pulchellus*; in BM *crassipes*; in USNM *gaimardi* and, from Hong Kong, *splendidus*; in Torino *gaimardi.*

Not Examined. More than 200 additional specimens in USNM, listed as *U. gaimardi*, from Samoa and the Society Is.

U. (*A.*) *chlorophthalmus chlorophthalmus* (Milne-Edwards, 1837)

EAST AFRICA. TANZANIA. *Pemba Island*: Kiburunzi (near Chake Chake): 30 m., 22 f. (NYZS). *Zanzibar*: (Muongoni): 13 m., 1 ovig. f. (NYZS). *Tanga*: Dar es Salaam near Kondeni (first stream north of city): 1 m. (NYZS).

MOZAMBIQUE. *Inhaca Island* (east lagoon): 9 m., 5 f. (NYZS).

INDIAN OCEAN. "Indian Ocean": 1 m. (Paris). *Mauritius*: Ile de France: "TYPE NON SPECIFIÉ" of *G. chlorophthalmus*, m. (Paris). Ile Maurice: small series of small m. & f. (Paris).

BRAZIL. Teffe on the Amazon: Type of *U. amazonensis* (Torino), m. *Locality certainly erroneous*; see p. 322.

Uca (*Amphiuca*) *inversa* (Hoffmann, 1877). (P. 105.)

U. (*A.*) *inversa inversa* (Hoffmann, 1877)

ETHIOPIA. Eritrea: 1 m. (Torino). Massawa: 16 m. (NYZS).

ARABIA. *Hadramaut*: Aden: 1 m. (BM part of series, gift of Yerberg). Mukalla: 1 m. (BM 88A).

SOMALILAND. Laguna di Honio: 1 m. (Torino).

KENYA. Near Lamu: 1 m. (BM 93.11.9.6).

TANZANIA. *Zanzibar*: Chakwani Fish Ponds: 84 m., 37 f. (NYZS).

MOZAMBIQUE. *Inhaca I.* (east lagoon): 4 m. (NYZS).

MADAGASCAR. Nossy Fally: LECTOTYPE of *G. inversus*, m. (Leiden 251; see comment on additional type material, p. 106).

NATAL. Perhaps from type material of *G. smithii*: 1 m. (Philadelphia 3003; labeled *inversa*).

Not Examined. A collection of more than 300 m. and f. from East Africa, near Mombasa, at Changawe and its strait (USNM 43465, 43466, 43467).

U. (*A.*) *inversa sindensis* (Alcock, 1900)

PAKISTAN. Mud between Karachi & Clifton (beyond refugee camp): 15 m. (NYZS).

SUBGENUS *BOBORUCA*

Uca (*Boboruca*) *thayeri* Rathbun, 1900. (P. 112.)

U. (*B.*) *thayeri umbratila* Crane, 1941

EL SALVADOR. La Herradura & La Union: type material of *U. thayeri zilchi* Bott, 1954 (Frankfurt: Senck. 2058, 2070). El Triunfo: 1 m. listed by Bott, 1954, as *U. t. thayeri*; has regenerated claw (Frankfurt: Senck. 2057).

COSTA RICA. Puntarenas: HOLOTYPE of *U. umbratila*, m. (NYZS 381,129 = USNM 138132); PARATYPE f. (NYZS 381,130 = USNM 138133). Golfito: 3 m., 5 f. (NYZS 38,509a; inadvertently omitted from Crane, 1941.1). Ballenas B.: 1 f. (NYZS 381,131).

PANAMA. Near Panama City: east of Old Panama, near mouth of Rio Abajo, by water pump: 2 m. (NYZS).

CANAL ZONE. Balboa at La Boca: PARATYPES of *U. umbratila*: 1 m., 1 f. (USNM 79407); 18 yg. m., 12 yg. f., 2 post-megalopal carapaces (NYZS 4118 = USNM 138134).

U. (*B.*) *thayeri thayeri* Rathbun, 1900

UNITED STATES OF AMERICA. *Florida*: St. Augustine: 3 m., 2 f. (NYZS). Miami: 1 m. (NYZS). Marco-Coxambas Cut (near Coon Key): 1 m., 1 f. (USNM 74493). Sanibel I.: 1 f. (MCZ 10183).

GUATEMALA. Puerto Barrios: 1 m. (NYZS).

GUADELOUPE. 2 ovig. f. (NYZS).

TRINIDAD AND TOBAGO. *Tobago*: near Pigeon Point: 3 m. (NYZS). *Trinidad*: near Port of Spain (Cocorite, Laventille & Caroni Swamps): 85 m., 72 (37 ovig.) f. (NYZS).

VENEZUELA. *Aragua*: Turiamo: 2 m. (NYZS). *Delta Amacuro*: Pedernales: 3 f. (NYZS).

BRAZIL. *Parahybo do Norte*: Parahybo R. at Cabedello. TYPES of *U. thayeri*: 7 m., 1 f. (USNM 23753). *Pernambuco*: Recife (swamp close to Olinda Causeway): 9 m., 3 (2 ovig.) f. (NYZS). *Bahia*: São Salvador [Bahia] (on Itaparica I.): 10 m., 3 f. (NYZS). Plataforma: 1 m., 1 f. (USNM 40619). *Rio de Janeiro*: east shore Ilya Pinheiro (lagoon): 2 m., 1 ovig. f. (NYZS).

Not Examined. About 50 additional specimens at USNM from various localities throughout the range of the subspecies.

SUBGENUS *AFRUCA*

Uca (*Afruca*) *tangeri* (Eydoux, 1835). (P. 118.)

PORTUGAL. *El Algarve*: Faro: 213 m., 75 (9 ovig.) f. (NYZS). Vila Réal de São Antonio: 4 m. (NYZS).

TANGIER. TYPE MATERIAL of *G. tangeri*, 1 m., 1 f. (Paris 3478-1, 3478-2; "types non specifiés"); 1 m., 1 f. (Paris 3477); 1 m. (Phil. Acad. 9-3028, from Guérin; "type").

"GUINEA COAST," probably including GHANA. "Boubry," "Acre d'Elmina," and "Kust van Guinea": type material of *G. perlatus* (Leiden 259, 260, 261, 262).

NIGERIA. Lagos (at Tarkwa B.): 29 m., 17 f. (NYZS).

CONGO. Banana: 44 m., 20 f. (AMNH 3071 part); 2 m., 2 f. (AMNH 3073); 5 m., 6 f. (AMNH 3075 part).

ANGOLA. Santo Antonio do Zaire: 1 m., 1 f. (AMNH 3072). Near Loanda: Samba: 68 m., 34 f. (NYZS): Samba Pequeña: 33 post-megalopal yg. (NYZS); Ilya de Cabo: 94 yg. m., 98 yg. f. (NYZS). Lobito: 6 m., 4 f. (AMNH 5916); 3 m., 2 f. (AMNH 5917 part).

WEST AFRICA. 2 m. (AMNH 5922); 14 m., 4 f. (AMNH 5933 part); 39 m., 17 f. (AMNH 5934 part); 10 m., 8 f. (AMNH 5935 part); 14 m., 3 f. (AMNH 5936 part).

Not Examined. More than 50 specimens at USNM from various localities in west Africa, between Dakar and Loanda.

SUBGENUS *UCA*

Uca (*Uca*) *princeps* (Smith, 1870). (P. 128.)

U. (*U.*) *princeps princeps* (Smith, 1870)

MEXICO. *Lower California*: *West Coast*: Santo Domingo: 1 m. (USNM 51107). Abreojos Point: 5 m., 3 f. (USNM 20689). *Gulf of California* (*South District*): La Paz: 1 m., 2 f., 1 yg. (USNM 14826). *Sonora*: Empalme: 2 m. (USNM 57066). *Nayarit* [*Tepic Terr.*]: San Blas: 1 yg. m., 1 yg. f. (USNM 99750); 6 m. (USNM 99751); 4 m. (USNM 99752); 1 m., 3 f. (USNM 20654).

NICARAGUA. Corinto: COTYPES of *G. princeps*, 9 m. + 3 m. (MCZ 5813, 5814).

COSTA RICA. Golfito: 2 m., 1 f. (NYZS 38588). Ballenas B.: 1 m. (NYZS 38355). Santo Domingo, Gulf of Dolce: 1 yg. m. (USNM 19440).

CANAL ZONE. Balboa (La Boca): 3 disintegrated specimens (NYZS 4135).

ECUADOR. Puerto Bolivar (near mouth of Guayas R.): 11 m., 3 f. (NYZS).

PERU. B. of Sechura: salt marshes back of Chulliyache: 3 m. (USNM 40467). Rio Zarumilla: salt flats at Puerto Grande: 1 m. (USNM 40468).

U. (*U.*) *princeps monilifera* Rathbun, 1914

MEXICO. *Gulf of California* (*North District*): San Felipe: 1 m., 1 f. (USNM 67735). Montague I. (mouth of Colorado River): 1 m. (USNM 48829). *Sonora*: Guaymas: HOLOTYPE of *U. monilifera*, m. (MCZ 1578) + 7 m. "out of type lot" (MCZ 8272); PARATYPE, m. (USNM 22180, received from MCZ, from 1578).

Uca (*Uca*) *heteropleura* (Smith, 1870). (P. 133.)

EL SALVADOR. Gulf of Fonseca: HOLOTYPE of *G. heteropleurus*, m. (MCZ 5819).

COSTA RICA. Punta Arenas: 1 yg. m. (USNM 39099). Golfito: 2 m., 2 f. (NYZS 38589).

PANAMA. Bahia Honda: 7 m., 5 f. (NYZS 38698). Panama City: 1 m. (NYZS 4138); Bellavista: 43 m., 14 f. (NYZS).

CANAL ZONE. Balboa: 2 m. (NYZS 4137).

ECUADOR. Puerto Bolivar (near mouth of Guayas R.): 8 m. (NYZS).

Uca (*Uca*) *major* (Herbst, 1782). (P. 136.)

WEST INDIES. *Bahamas*: Bimini: 1 m., 1 f. (USNM 91740). *San Salvador* or *Watling's Island*: 2 m., 1 f. (USNM 11375); 1 m. (MCZ 6366). *Cuba*: Baracoa: 6 m., 1 f. (USNM 25549). *Jamaica*: 1 m. (USNM 42918). *Guadeloupe*: Type of *G. grangeri* ("type non specifié"), 1 f. (Paris). *Trinidad*: 1 m. (NYZS; gift of H. O. von Hagen). *Curaçao*: Carmabi: 1 m. (NYZS; gift of A.C.J. Burgers).

CANAL ZONE. Colon: 1 yg. m. (USNM 57744).

VENEZUELA. *Aragua*: Turiamo: 3 m. (NYZS).

CAYENNE. Type of *G. platydactylus* ("type non specifié"), 1 m. (Paris).

Uca (*Uca*) *stylifera* (Milne-Edwards, 1852). (P. 140.)

NICARAGUA. Gulf of Fonseca: Cotypes of *G. heterophthalmus*, 4 m. (MCZ 5818). West coast: 2 m. (USNM 74428). Corinto: 4 m., 1 f. (NYZS 3813); 2 f. (MCZ 5815 part; published by Smith, 1870: 126, as *U. ? princeps*; third specimen is missing).

COSTA RICA. Puntarenas: Pacific-Estero side: 2 m. (USNM 32325). Punta Arenas: 1 m. (USNM 61592). Golfito: 8 m., 9 (1 ovig.) f. (NYZS 38589).

CANAL ZONE. Balboa (La Boca): 2 m. (NYZS 4136).

ECUADOR. Guayaquil: LECTOTYPE of *G. styliferus* ("type non specifié"), 1 m. (Paris). Puerto Bolivar (near mouth of Guayas R.): 1 m. (NYZS).

Uca (*Uca*) *maracoani* (Latreille, 1802-1803). (P. 143.)

U. (*U.*) *maracoani maracoani* (Latreille, 1802-1803)

WEST INDIES. *Santo Domingo*: Sanchez: 1 f. (AMNH 2466). *Trinidad*: Port of Spain (Cocorite): 16 m., 16 (1 ovig.) f. (NYZS).

VENEZUELA. *Delta Amacuro*: Pedernales: 14 m., 3 f. (NYZS 42414).

GUYANA. Near Georgetown: 1 m. (AMNH 4637). Georgetown: 2 m., 1 f. (AMNH 6645); mouth of Demerara R. and Kitty Village: 3 m., 2 f. (NYZS); Kitty Village: 26 m., 18 (3 ovig.) f. (NYZS).

BRAZIL. *Maranhão*: 13 m., 5 f. (USNM 17657 part); 2 m., 2 f. (USNM 22190). Tutoya Creek: 4 m., 1 ovig. f. (AMNH 4657). *Rio Grande do Norte*: Natal: 6 m., 1 f. (USNM 25697). *Bahia*: São Salvador [Bahia]: Bahia de Todos Santos: Ilya Itaparica: 1 m., 1 f. (NYZS). Porto Seguro: 2 m., 1 f. (USNM 22191). Plataforma: 4 m., 3 f. (USNM 40613); 7 m., 2 f. (USNM 40614). *Parana*: Paranagua: 1 m. (USNM 71177).

U. (*U.*) *maracoani insignis* (Milne-Edwards, 1852)

NICARAGUA. Gulf of Fonseca: Type of *G. armatus*, 1 m. (MCZ 5816).

ECUADOR. Puerto Bolivar (mouth of Guayas R.): 5 m., 1 f. (NYZS).

PERU. Piura (mud flats at mouth of Rio Tumbez): 1 m. (USNM 71321); Chulliyache (B. of Sechura; salt marshes): 1 m. (USNM 40489).

"CHILI." HOLOTYPE of *Acanthoplax insignis* ("type non specifié"), f. (Paris).

Uca (*Uca*) *ornata* (Smith, 1870). (P. 150.)

WEST COAST OF CENTRAL AMERICA. HOLOTYPE of *G. ornatus*, f. (MCZ 5817).

COSTA RICA. Puntarenas: 1 m. (USNM 61036).

PANAMA. Mouth of Rio Abajo (near Old Panama): 4 m., 1 ovig. f. (NYZS; gift of M. D. Burkenroad); 25 m., 31 (3 ovig.) f. (NYZS). Panama City: (Bellavista): 1 m. (NYZS 4140).

CANAL ZONE. Balboa (La Boca): 2 m., 1 yg. f. (NYZS 4139).

PERU. Puerto Pizarro: holotype of *U. pizarri*, m. (Leiden D 23061) + paratype, 1 m. (Leiden D 23062).

SUBGENUS *MINUCA*

Uca (*Minuca*) *panamensis* (Stimpson, 1859). (P. 158.)

NICARAGUA. Gulf of Fonseca, near Potosi R.: 2 m., 1 yg. f. (NYZS 37701). Corinto: Cardon: 9 m., 5 f. (NYZS 37735).

COSTA RICA. Port Parker: 7 + 1 yg. m., 8 + 2 yg. f. (NYZS 3861 & 3892). Culebra B.: 1 m. (NYZS 38119). Piedra Blanca: 5 m., 4 f. (NYZS 38166); 3 m., 3 f. (NYZS 38197). Ballenas B.: 1 f. (NYZS 38345). Uvita B.: 5 m., 3 yg. f. (NYZS 38456). Golfito: 7 m., 5 f. (NYZS 38517).

PANAMA. Bahia Honda: 3 m., 1 f. (NYZS 38706). Patillo Point: 9 m., 8 f. (AMNH 5974); 4 m. (AMNH 6642); 2 f. (AMNH 6663). Panama B.: north shore Tabogilla I.: 2 m., 6 f. (AMNH 5978); 1 yg. f. (AMNH 5985). Pearl Is.: Pacheca I.: 2 m., 1 f. (AMNH 5983). Panama City: 1 yg. m., 2 yg. f. (poor condition) (NYZS 4149).

COLOMBIA. Gorgona Island: Gorgonilla: 4 m., 4 (2 ovig.) f. (NYZS 38855); 13 m., 9 f. (NYZS 38878). Humboldt B.: 9 m., 2 f. (AMNH 10703); 1 m. (AMNH 10704).

PERU. Payta: 4 m., 1 f. (MCZ 5908).

Not Examined. About 15 additional specimens at USNM from within the range of the species.

Uca (*Minuca*) *pygmaea* Crane, 1941. (P. 161.)

COSTA RICA. Golfito: HOLOTYPE of *U. pygmaea*, m. (NYZS 381,110 = USNM 137419); PARATYPES, 10 m. (NYZS 381,111, part = USNM 137420), 2 m. (NYZS 381,111, part = USNM 79402).

COLOMBIA. Buenaventura: 1 m. (NYZS; gift of T. Collett, U. of London).

Uca (*Minuca*) *vocator* (Herbst, 1804.) (P. 163.)

U. (*M.*) *vocator vocator* (Herbst, 1804)

MEXICO. *Vera Cruz*: Tampico: 1 m. (USNM 43353 part). Arroyo de la Renal, tributary of Tonchochapa R.: 1 m. (NYZS: gift of G.A.W.).

BRITISH HONDURAS. Near Belize: 1 m. (USNM 21373 part).

GUATEMALA. Puerto Barrios: 3 m., 2 f. (NYZS).

NICARAGUA. Greytown: 1 m. (USNM 18434 part).

WEST INDIES. *Santo Domingo*: Sanchez: 1 f. (MCZ 9860 part); 1 m., 2 f. (AMNH 2441 part). *Puerto Rico*: San Juan: 2 m., 1 f. (NYZS), 1 m. (AMNH 2690). *Guadeloupe*: 1 m. (NYZS). *Trinidad*: Blanchisseuse (north coast): 1 m. (NYZS). Cocorite Swamp (near Port of Spain): 2 yg. m. (NYZS). Behind pump station, Caroni Swamp: 5 m. (NYZS). Caroni Swamp: 4 m. (NYZS). Lavantille Swamp: 4 m. (NYZS). Near stream mouth, Manzanillo (east coast): 2 m. (NYZS).

VENEZUELA. *Zulia*: Maracaibo: 14 m., 1 f. (NYZS 42419; published as *U. murifecenta* in *Zoologica* 28 (7): 38; 1943); 2 f. (NYZS 42421 part; published as *U. pugnax rapax, loc. cit.*). Lagunillas: 4 m., 4 f. (NYZS). *Sucre & Monagas*: near mouth of San Juan R.: holotype of *U. murifecenta*, m. (NYZS 42167 = USNM 137424); paratypes of *U. murifecenta*, 5 m., 6 f. (NYZS 42417 = USNM 137425); 25 m., 20 (3 ovig.) f. (NYZS 42418; published as *U. murifecenta, loc. cit.*). *Delta Amacuro*: Pedernales: specimens wholly desiccated, pulverized; discarded (NYZS 42416; published as *U. murifecenta, loc. cit.*).

GUYANA. Georgetown: Kitty Village (flats near seawall): 10 m., 5 (1 ovig.) f. (NYZS); foot of Kitty Village: 1 f. (NYZS).

BRAZIL. *Estado Rio de Janeiro*: Serra de Masaché: 2 m. (USNM 50690 part).

SURINAME. Shore of Suriname R., near Leonsburg, north of Paramaribo: NEOTYPE of *U. vocator*, m. (Leiden 1208).

U. (*M.*) *vocator ecuadoriensis* Maccagno, 1929

MEXICO. *Nayarit* [*Tepic Terr.*]: San Blas: holotype of *U. schmitti*, m. (USNM 80451 out of 22306, formerly labeled *U. mordax*) + paratypes, 3 m. (USNM 22306, also formerly labeled *U. mordax*); 1 m. (USNM 99756). *Guerrero*: Acapulco: paratype of *U. schmitti*, 1 m. (MCZ 5892, part, formerly labeled *U. mordax*).

NICARAGUA. San Juan del Sur: paratype of *U. schmitti*, m. (NYZS 381,116 = USNM 137421) published first as *U. mordax* in *Zoologica* 26 (19): 176; 1941.1); 1 yg. m. (NYZS 381,120; published first 1941.1, *loc. cit.*, as *U. brevifrons*).

COSTA RICA. Negritos I.: paratype of *U. schmitti*, m. (NYZS 381,117 = USNM 137423) published first as *U. mordax, loc. cit.* Golfito: paratype of *U. schmitti*, m. (NYZS 381,118 = USNM 137422) published first as *U. mordax, loc. cit.*); 2 m. (NYZS).

PANAMA. Bahia Honda: 5 m., 1 f. (NYZS 38681; omitted from *Zoologica* 26 (19); 1941).

COLOMBIA. Buenaventura: 2 m., 2 f. (USNM 158,353, part); 1 m. (NYZS: gift of T. Collett, U. of London); 2 m., 2 f. (NYZS; gift of Brother Iñez, Bogotá, Colombia).

ECUADOR. Esmeraldas: TYPE MATERIAL of *U. ecuadoriensis*, 2 yg. m. (Torino); 1 m. (USNM 98041). Puerto Bolivar: 6 m., 6 f. (NYZS). Guayaquil: 1 m. (USNM 70867); El Salado: 1 m. (USNM 98039); 96 m., 20 (8 ovig.) f. (NYZS). Near Guayaquil: 3 m. (USNM 98038).

PERU. Puerto Pizarro: holotype of *U. lanigera*, m. (Leiden D 23049); paratypes, 10 m., 5 f. (Leiden D 23050).

Uca (*Minuca*) *burgersi* Holthuis, 1967. (P. 168.)

UNITED STATES. *Florida*: Ft. Lauderdale (Dania Beach, mangroves to south): 3 m. (NYZS).

MEXICO. Yucatan: Progreso: 20 m., 10 f. (MCZ 8628); 2 m., 2 f. (USNM 81381); near Telchac—P. Motul: m. + ? yg. (USNM 95526 part).

BRITISH HONDURAS. Belize: Yarborough: Loyola Park: 1 m. (NYZS; gift of collectors C. Fairweather and J. Lopez). Near Belize: 2 f. (USNM 21373 part); 8 m. (USNM 22604 part).

GUATEMALA. Puerto Barrios: 12 m., 2 f. (NYZS).

CANAL ZONE. Toro Point: 2 m. (USNM 59307).

WEST INDIES. *Swan I.*: 6 m. (MCZ 8392). *Cuba*: Santa Clara: Damuge R.: 11 m., 4 f. (AMNH 3166); Isla Turiguano: 10 m., 1 yg. f. (NYZS; gift of W.R.W. Riggs). *Bahamas*: Abaco I.: near Water Cay: 1 m. (MCZ 8632). Andros I.: 9 m., 3 f. (AMNH 2527); Mangrove Cay: 1 f. (MCZ 8643). East side Long I.: Grays: 65 m., 9 f. (MCZ 9440). Great Inagua I.: Mathew Town: 23 m., 10 f. (MCZ 10333); Savannah 3 mi. N. of Mathew Town: 11 m., 10 (3 ovig.) f. (MCZ 10361). *Haiti*: Manneville: 12 m., 6 (1 ovig.) f. (MCZ 8690). Near Port-au-Prince: Etang Saumâtre: 1 m. (NYZS; collected by W. Beebe). *Santo Domingo*: Sanchez: 28 m., 20 (5 ovig.) f. (AMNH 2444). Monte Cristi: 1 m. (MCZ 9880 part). *Puerto Rico*: San Juan: 13 m., 4 f. (AMNH 2983). Enseñada: 1 m., 1 f. (AMNH 2984 part); 2 m. (AMNH 3011 part). *Virgin Islands*: St. Croix: Buck Island Swamp: 3 m., 1 f. (NYZS; gift of H. Beatty). St. Thomas: 13 m. (NYZS); Red Hook: 81 m., 78 f. (NYZS). *St. Martin*: Crab Hole Cistern: 2 m., 2 ovig. f. (NYZS; gift of P. W. Hummelinck); Little B. Pond, east: 4 m., 4 ovig. f. (NYZS; gift of Dr. Hummelinck); pond of Point Blanche: 2 m. (NYZS; gift of Dr. Hummelinck). *Antigua*: 2 m., 3 f. (AMNH 2505). *Barbados*: Payne's B. (St. James Sector): 45 m., 18 (2 ovig.) f. (NYZS); 40 m., 9 f. (NYZS). *Tobago*: Pigeon Point Swamp (across road from beach): 28 m., 6 (1 ovig.) f. (NYZS). *Trinidad*: Blanchisseuse (north coast): 6 m., 2 f. (NYZS); sandy ground near Nariva Swamp Bridge: 1 m. (NYZS; gift of H.-O. von Hagen). *Aruba*: Balashi, by Spaans Lagoen (mangrove swamp): 1 f. (NYZS; gift of P. W. Hummelinck). *Curaçao*: HOLOTYPE of *U. burgersi*, m. (Leiden D 23012). *Jamaica*: 1 m. (USNM 18533).

VENEZUELA. *Aragua*: Turiamo: 7 m. (NYZS). *Miranda*: Laguna de Tacarigua: 1 m. (NYZS; gift of W. H. Phelps, Sr.).

BRAZIL. *Céara*: Fortaleza (semi-closed swamp beside Avenida Getulio Vargas): 30 m., 8 f. (NYZS). *Bahia*: São Salvador [Bahia]: Bahia de Todos Santos: Ilya Itaparica: 5 m., 1 f. (NYZS). *Rio de Janeiro*: 2 m., 2 f. (USNM 19971); Ilya Pinheiro: 4 m. (NYZS), Niterói [Nictheroy]: 1 m. (USNM 74436). *São Paulo*: Santos: São Sebastião: 4 m. (NYZS; gift of F. J. Vernberg); Ilya Bela: 1 m. (USNM 74437).

Locality and identification questionable. AFRICA: CAMEROONS: Metet: 3 yg. m., major chelipeds missing; 1 f. (MCZ 8962). LIBERIA: 1 f. (USNM 21847). See p. 327.

Not Examined. Numerous additional specimens at USNM from the West Indies, labeled *Uca mordax.* Casual inspection of sample jars shows these specimens to be *U. burgersi.*

Uca (Minuca) mordax (Smith, 1870). (P. 173.)

GUATEMALA. Puerto Barrios: 3 m., 2 f. (NYZS).

NICARAGUA. Greytown: 8 m., 2 f. (USNM 18433).

COLOMBIA. Turbo: 2 m. (MCZ 5891).

VENEZUELA. *Zulia*: Lagunillas: 1 m. (NYZS). *Monagas*: Caripito: 8 m., 1 f. (NYZS 4252); 22 m., 18 (4 ovig.) f. (NYZS). *Sucre*: Guanoco: 35 m., 24 f. (NYZS 4254). *Sucre & Monagas*: near mouth of San Juan R.: 26 m., 17 f. (NYZS 42166). *Delta Amacuro*: Tapure, near Pedernales: 74 m., 47 (4 ovig.) f. (NYZS 42415); 2 yg. m., 1 yg. f. (NYZS 42420 part). *Curiapo*: 1 m., 1 f. (USNM 95992).

TRINIDAD. Blanchisseuse, north coast of Trinidad: 1 m., 1 f. (NYZS); near mouth of Oropouche R., eastern Trinidad: 3 m., 1 f. (NYZS).

GUYANA. Georgetown: 2 m. (NYZS collected by W. Beebe); foot of Kitty Village: 2 m., 2 f. (NYZS).

SURINAME. Near Paramaribo: 14 m., 13 (2 ovig.) f. (NYZS); 18 m., 9 f. (NYZS). Mouth of Marawyne R. (West Indian Coconut Plantation): 41 m., 12 f. (NYZS).

BRAZIL: Maranhão: Pará: Belém (canals in city): COTYPES of *G. mordax*, 7 m., 5 f. (MCZ 5882); 50 m., 10 f. (NYZS). Itabapuana: 4 m., 4 f. (USNM 22186). *Pernambuco*: Recife [Pernambuco]: 1 m. (USNM 25698). *Rio de Janeiro*: "Terra de Masahe" [Serra de Masaché]: 2 m. (USNM 47834).

Uca (Minuca) minax (LeConte, 1855). (P. 176.)

UNITED STATES. *Massachusetts*: Wareham: 1 f. (AMNH 1028). *Connecticut*: Old Lyme: 10 m., 5 f. (NYZS). Clinton: 1 m. (AMNH 6490). *New Jersey*: Dennis Creek: apparent TYPE MATERIAL of *G. minax*, 2 m., 1 f. (Philadelphia Academy 3581). Lower Alloway Creek near Quinton: 11 m., 15 f. (NYZS). *Florida*: Jacksonville: 8 m., 9 f. (AMNH 3986); 11 m. (AMNH 3981). Key West: 2 m. (MCZ 5900). Pensacola: 1 m. (MCZ 5901). *Alabama*: Mobile B.: 1 m. (USNM 21681). *Mississippi*: west end of Back B. Bridge, east Biloxi: 1 m., 1 f. (USNM 90302). Ocean Springs on Biloxi B.: 4 m., 2 f. (USNM 101102). *Louisiana*: Pont Chartrain: Point Platte: 1 f. (USNM 98144). Cameron: 1 m. (USNM 30570). Chauvin: 2 m. (AMNH 9800); 10 m., 33 f. (AMNH 9814). Gulf of Mexico, south of Morgan City: 5 f. (AMNH 9831).

Uca (Minuca) brevifrons (Stimpson, 1860). (P. 180.)

MEXICO. *Lower California (South District)*: west coast (near Cape St. Lucas): lagoon at Todos Santos: from TYPE LOT, 1 f. (MCZ 1332). *Guerrero*: Acapulco: 3 m. (MCZ 5910); 1 claw (MCZ 5892 part). Puerto Angeles: 1 claw (NYZS 381,119).

COSTA RICA. Port Porker: 5 m., including yg. + claws, 4 f. (NYZS 381122). Negritos I.: 3 m. + growth series, including 23 yg. m. and f. (NYZS

381123). Cocos I.: 1 f. (USNM 63152). Uvita B.: 3 m., 2 f. (NYZS 381124). Golfito: 2 m., 1 f. (Torino); 1 + 2 yg. f. (NYZS 381125). Quebrada Chavarria: 3 m., 4 f. (USNM 19435). Boca del Rio Jésus Maria: 1 m. (USNM 32323); 1 m., 1 f. (USNM 32324). Pigres: 9 m., 1 f. (USNM 43352). Parida I.: 2 m., 2 f. (NYZS 381126).

PANAMA. "Panama": 6 m., 2 (1 ovig.) f. (MCZ 5909); 1 m. (USNM 22185). Yarisa: 2 m. (AMNH 6641). Banks of Rio Piñas: Piñas B.: 8 m., 1 f. (AMNH 10702). Darien: Rio Lara: holotype of *U. brevifrons* var. *delicata*, m. (Torino). Marraganti: 1 m. (USNM 48277). Rio Calabre: 4 m. (USNM 43988).

CANAL ZONE. La Capitana: 1 m. (USNM 43848); 3 m. (USNM 44320); 2 large claws (USNM 49097).

Uca (Minuca) galapagensis Rathbun, 1902. (P. 183.)

U. (M.) galapagensis herradurensis Bott, 1954

MEXICO. *Sonora*: Guaymas: ? 1 m. (MCZ 5913). *Jalisco*: Tenacatita B.: ? 1; very yg. in poor condition, discarded (NYZS 381,127; published as *U. macrodactyla* in *Zoologica*: 26 (19): 178; 1941).

EL SALVADOR. La Herradura: HOLOTYPE of *U. herradurensis*, m. (Frankfurt 1865). Los Blancos: holotype of *U. macrodactyla glabromana*, yg. m. (Frankfurt 1842).

NICARAGUA. Corinto: 2 m., 1 f. (MCZ 5912); 12 m., 1 f. (NYZS 381,128; published as *U. macrodactyla*, *loc. cit.*).

COSTA RICA. Boca del Rio Jésus Maria: 1 m., 1 f. (USNM 32320).

PANAMA. Near Panama City: 1 m. (AMNH 5979); 2 yg. m. (AMNH 5984). Between Patillo Point and Old Panama: 1 m. (AMNH 5992). Rio Abajo (swamp near mouth; near Old Panama): 89 m., 17 (1 ovig.) f. (NYZS).

U. (M.) galapagensis galapagensis Rathbun, 1902

COLOMBIA. Tumaco: 1 yg. m., subspecies questionable (Torino); Tumaco (Puntilla Sta. Elena): 1 m. (Torino).

ECUADOR. *Galapagos Is.*: Indefatigable I.: HOLOTYPE of *U. galapagensis*, m. (USNM 22319) + 5 additional m. under same number; 1 m. (NYZS 2367). James I.: 3 m., 1 f. (USNM 57743); 1 m. (NYZS 2624 part). Eden I.: 1 m. (NYZS 2042; see p. 188). Guayaquil: 16 m., 10 (1 ovig.) f. (NYZS). Puerto Bolivar (mouth of Guayas R.): 17 m., 18 f. (NYZS).

PERU. Puerto Grande on Zarumilla R. (near Capon salt flats): 1 m. (MCZ 12179).

[CHILE. Valparaiso: ? type material of *G. macrodactylus* (Paris; see p. 186).]

Not Examined. A few additional specimens at USNM from within the ranges of both subspecies and catalogued under the names of *U. galapagensis* and *U. macrodactylus.*

Uca (Minuca) rapax (Smith, 1870). (P. 190.)

U. (M.) rapax rapax (Smith, 1870)

UNITED STATES. *Florida*: Ft. Lauderdale: Dania Beach (mangroves to south): 3 m. (NYZS); Miami: Key Biscayne (St. V mudbank drainage): 2 m. (NYZS; gift of U. of Miami, Oceanographic Lab. Collector: H. K. Voris); causeway to Tahiti Beach, south Miami: 13 m., 8 f. (NYZS); 18 m., 8 f. (NYZS). Everglades: 2 m. (AMNH 2523).

MEXICO. *Tamaulipas*: Laguna de la Madre Austral: 3 miles south of south point of rocks: 1 m., 2 (1 ovig.) f. (USNM 96475).

GUATEMALA. Puerto Barrios: 22 m., 4 f. (NYZS).

BRITISH HONDURAS. *Belize*: 2 m., 2 f. (USNM 22604 part); 1 m., 1 f. (USNM 50950). Loyola Park, Yarborough: 23 m., 6 f. (NYZS; gift of C. Fairweather & J. Lopez).

CANAL ZONE. Fort Randolph, Galeta Pt.: 6 m. (USNM 89572).

WEST INDIES. *Bahamas*: Andros I.: 30 m. (AMNH 2449). *Haiti*: Bizoton: 8 m. (NYZS 27273; collected by W. Beebe). *Santo Domingo*: Sanchez: 5 m., 1 f. (MCZ 9860 part); 23 m., 14 (1 ovig.) f. (AMNH 2441 part). Monte Cristi: 6 m. (MCZ 9880 part). *Puerto Rico*: Enseñada: 3 m., 4 f. (AMNH 3011 part); 1 m. (AMNH 2984 part). Ponce: 4 m. (AMNH 3012); 22 m., 20 f. (NYZS). San Juan: 5 m., 1 f. (AMNH 3013); 69 m., 14 (8 ovig.) f. (NYZS). *Virgin Is.*: St. Thomas: 100 m., 17 f. (NYZS); Red Hook: 1 m. (NYZS; gift of Dr. Hummelinck). *Tobago*, near Pigeon Point: 3 m., 3 (1 ovig.) f. (NYZS); 4 m. (NYZS); 43 m., 5 (1 ovig.) f. (NYZS). *Trinidad*: Blanchisseuse (north coast): 3 m. (NYZS). Chacachachari I.: 1 m. (AMNH 2452). Port of Spain and vicinity: 2 m. (AMNH 2530); 7 yg. f. (NYZS); 4 f. (NYZS); Diego Martin R.: 127 m. (NYZS); Cocorite Swamp: 11 yg. m. (NYZS); 88 m. (NYZS): Laventille and Cocorite Swamps: 46 m. (NYZS). Monkey Point, near San Fernando: 4 m. (NYZS). *Curaçao*: Carmabi: 3 m., 1 f. (NYZS; gift of A.C.J. Burgers). *Aruba*: Spaans Lagoen, Balashi: 3 m., 1 f. (NYZS: gift of P. W. Hummelinck). *Jamaica*: 1 m., 2 f. (USNM 18553); 1 m. (USNM 22307).

COLOMBIA. Cartagena: 14 m., 9 f. (NYZS).

VENEZUELA. *Zulia*: Maracaibo: 425 m., 73 f. (NYZS 42421, 42422, 42426, 42427, parts; 5 collecting stations from Yacht Club and vicinity extending 4 miles north. Note: Maracaibo collection made during World War II and necessarily preserved in rum in the field. Many specimens in poor condition but saved because of potential future use in studies of growth and variation). Lagunillas: 1 m. (NYZS). *Yaracuy*: mouth of Yaracuy R.: 1 m. (NYZS). *Carabobo*: Puerto Cabello: 54 m., 26 f. (NYZS). *Aragua*: Turiamo: 31 m., 11 (1 ovig.) f. (NYZS). Islas Los Roques: 4 m., 3 f. (NYZS; gift of W. H. Phelps, Sr.); 33 m., 7 f. (NYZS: gift of W. H. Phelps & A. L. Haight). *Miranda*: Laguna de Tacarigua: 11 m. (NYZS: gift of W. H. Phelps, Sr.). *Anzoa-Tegui*: Puerto la Cruz: 2 m. (NYZS). *Sucre & Monagas*: near mouth of San Juan R.: 8 m., 9 (2 ovig.) f. (NYZS 42168). *Delta Amacuro*: Pedernales: 73 m., 32 (1 ovig.) f. (NYZS 42420).

GUYANA. Georgetown (foot of Kitty Village): 24 m., 6 f. (NYZS); 194 m. (including 66 with claws attached), 16 f. (NYZS).

SURINAME. Near Paramaribo (near river mouth): 13 m., 2 f. (NYZS).

BRAZIL. *Maranhão*: São Luiz (swamp paralleling Avenida Getulio Vargas, behind mental hospital): 36 m., 2 f. (NYZS). *Céara*: Fortaleza: (semi-closed swamp beside Avenida Getulio Vargas): 4 m. (NYZS). *Pernambuco*: Recife [Pernambuco] (swamp before beginning of Olinda Causeway): 11 m., 5 (1 ovig.) f. (NYZS). *Bahia*: São Salvador [Bahia]: Bahia de Todos Santos: Ilya Itaparica: 4 m., 1 f. (NYZS). *Rio de Janeiro*: Ilya Pinheiro: 83 m., including 59 with claws attached), 29 (1 ovig.) f. (NYZS); Serra de Masaché: 1 m. (USNM 50690).

Not Examined. Numerous additional specimens at USNM from many localities within the range of the subspecies; they are catalogued under the names *U. pugnax rapax* and *U. rapax*; also a few small specimens at AMNH, similarly catalogued.

U. (M.) rapax longisignalis Salmon & Atsaides, 1968

UNITED STATES. *Florida*: Yankeetown: 14 m., 3 f. (NYZS; gift of M. Salmon). *Mississippi*: coast of Mississippi: 1 m. (USNM 74902). Ocean Springs:

HOLOTYPE of *U. longisignalis*, m. (USNM 121599), PARATYPES, 5 m. (USNM 122204); 2 m. (NYZS; gift of M. Salmon); 4 m., 2 f. (USNM 215461); Biloxi B.: 1 m. (USNM 21845). *Louisiana*: near New Orleans: Grand Isle: 3 m. (USNM 2259). *Texas*: Galveston: Offat's Bayou: 1 m. (USNM 82110 part). Matagorda B.: 1 m. (MCZ 12178); 13 m., 1 f. (USNM 33035).

Uca (Minuca) pugnax (Smith, 1870). (P. 200.)

U. (M.) pugnax pugnax (Smith, 1870)

UNITED STATES. *Massachusetts*: Amamesse I.: Hadley Harbor: 8 m., 4 f. (AMNH 1031). Cape Cod: near Provincetown: SW of Telegraph Hill: 3 m. (NYZS, July, 1972); mouth of Little Pamet R.: 1 m. (NYZS, July, 1972). Harwich: 12 m., 1 f. (NYZS; gift of G. Cuyler); Woods Hole: 6 m., 2 f. (AMNH 97); North Falmouth: 36 m. (AMNH 1030); 1 m. (AMNH 1027 part). Martha's Vineyard: Katona B.: 5 m., 1 f. (AMNH 2435). Wareham: 7 m., 8 f. (AMNH 1026). *Connecticut*: New Haven: TYPE MATERIAL of *G. pugnax*, 1 m. (Yale 1060). *New York*: Oyster B.: 36 m., 15 f. (NYZS). Fire Island: 2 m. (AMNH 9358). Sheepshead B.: 1 m. (AMNH 2454). Staten Island: Princes B.: 29 m., 9 (mostly ovig.) f. (AMNH 2447). *New Jersey*: Bergen Beach: 6 m. (AMNH 2438); 3 m. including 1 yg. (AMNH 2440); 1 m. (AMNH 2610); 11 f. (AMNH 6119). West Keansburg: 1 f. (AMNH 2611). Near Brigantine: 11 m. including 3 yg., 10 f. including 1 yg. (NYZS). *Florida*: St. Augustine: 29 m., 8 f. (NYZS).

Not Examined. Numerous additional specimens at USNM from many localities throughout the range of the subspecies.

U. (M.) pugnax virens Salmon & Atsaides, 1968

UNITED STATES. *Louisiana*: Cameron: 1 m. (USNM 30570). *Texas*: Matagorda B.: 1 m. (USNM 33031). Port Aransas: HOLOTYPE of *U. virens*, m. (USNM 121598); PARATYPES, 5 m. (USNM 122205); 3 m. (NYZS; gift of M. Salmon); 2 m., 1 f. (NYZS; gift of M. Salmon). Texas coast: 4 m., 1 ovig. f. (USNM 72132); "Gulf coast, Texas": 1 m., 1 f. (USNM 72131). Corpus Christi: 7 m. (NYZS).

MEXICO. *Tamaulipas*: Tampico: 1 m. (USNM 18689); 4 m. + ? 1 juv. m. (USNM 43353 part). *Vera Cruz*: Arroyo de la Renal, tributary of Tonchochapa R. (Tonala drainage): 10 m., 6 f. (NYZS; gift of G.A.W.). Arroyo Amate of Uxpanapa R. of Coatzacoalcos (drainage ca. 8 km east of Minatitlan): 2 m. (NYZS; gift of G.A.W.); 8 km from Coatzacoalcos on new road to Minatitlan: 2 f. (NYZS; gift of G.A.W.).

Uca (*Minuca*) *zacae*
Crane, 1941. (P. 206.)

NICARAGUA. Corinto: 2 m., 2 f. (NYZS 381,114 = USNM 79408). San Juan del Sur: 2 m. (NYZS 381,115).

COSTA RICA. Golfito: HOLOTYPE of *U. zacae*, m. (USNM 137426, formerly NYZS 381,112); PARATYPES, 16 m., 11 f. (USNM 137427, formerly NYZS 381,113); 1 m. (NYZS). Cocos I: ? 2 m., ? 1 f. (U. of Southern California, Allan Hancock Foundation; see p. 207).

Uca (*Minuca*) *subcylindrica*
(Stimpson, 1859). (P. 209.)

UNITED STATES. *Texas*: Corpus Christi: 1 m. (USNM 23655). 3 miles south of Armstrong: Kenedy Co.: 4 m. (USNM 99826). Cameron Co.: near Santa Rosa: 1 m. (USNM 17807).

MEXICO. Matamoros (on the Rio Grande): COTYPES of *G. subcylindricus*, 1 m., 3 f. (MCZ 1327). "Mexico": 2 m. (Paris. Perhaps also COTYPES; see p. 210).

SUBGENUS *CELUCA*

Uca (*Celuca*) *argillicola*
Crane, 1941. (P. 220.)

COSTA RICA. Golfito: HOLOTYPE of *U. argillicola*, m. (NYZS 381,134 = USNM 137400); PARATYPES, 2 f. (NYZS 381,135 = USNM 137401).

PANAMA. *Pearl Is.*: San José (banks lower Marina R.): 2 m. (AMNH 9873).

COLOMBIA. Buenaventura: several specimens identified with certainty but not preserved (NYZS).

Uca (*Celuca*) *pugilator*
(Bosc, 1801-1802). (P. 223.)

UNITED STATES. *Massachusetts*: Cape Cod: Truro or Corn Hill: 1 m. (USNM 43355); mouth of Little Pamet R.; 1 m. (NYZS, July, 1972); North Falmouth: 85 m., 12 f. (AMNH 1027 part). *New York*: Long Island: Easthampton: 7 m., 2 f. (AMNH 2405); near Oyster B.: 15 m., 8 f. (NYZS). New York Harbor: 2 m. (AMNH 55). *New Jersey*: Bergen Beach: Growth series of yg. (AMNH 2613). West Keansburg: 1 yg. (AMNH 2560). *Florida*: 5 m. (AMNH 2387). Ft. Lauderdale (Dania Beach, mangroves): 2 m., 2 f. (NYZS). Miami: 5 m., 2 f. (AMNH 3014). Key West: 2 m. (USNM 18552). Punta Gorda: 1 m. (AMNH 2600); 3 m., 1 f., 1 yg. (AMNH 2631); growth series of yg. (AMNH 2886). Seven Oaks: 2 m. (AMNH 2389). *Texas*: Galveston: Offat's Bayou: 1 m. (ex-USNM 82110). Corpus Christi: 3 m., 1 f. (NYZS).

WEST INDIES. *Bahamas*: Andros I.: 1 m., 1 f. (AMNH 2406).

? SANTO DOMINGO. 2 yg. males. (AMNH 2555; *locality questionable*; see p. 226).

Not Examined. The USNM has a large collection of additional specimens from many localities on the eastern and southern coasts of the United States. All of these records fall within the boundaries of the examples listed above. Most of the catalogue numbers apply to single specimens or to short series numbering fewer than 10 of both sexes. Exceptionally large series include the following: *Massachusetts*: Woods Hole: 85+ specimens (USNM 3212). *Virginia*: Smiths Island: 34 m., 41 f. (USNM 74452, 74453). *North Carolina*: Beaufort: 25+ yg. specimens (USNM 54471); Gallant Point: Beaufort Harbor: 30+ specimens (USNM 63329). *South Carolina*: "South Carolina": 65 m., 62 f. (USNM 2061); Charleston: 30 m., 9 f. (USNM 3148). *Florida*: Pine Key: 79 m., 7 f. (USNM 6440); Big Gasparilla Pass: 26 m., 23 f. (USNM 15253).

Uca (Celuca) uruguayensis Nobili, 1901. (P. 229.)

BRAZIL. *Rio de Janeiro*: 2 m., 1 f. (USNM 40624); Guanabara B.: Ilya Pinheiro: 11 m., 2 f. (NYZS); Ilya Pinheiro (south side by wharf): 14 m., 7 f. (NYZS); Paqueta: 21 m. + 2 claws (USNM 71181); 4 m. (USNM 71182 part); 1 m. (USNM 71183 part). *São Paulo*: Santos: E. Piassaguera: 1 m. (USNM 47870); Santos Estuary, between canals 4 and 5: 15 m. (USNM 71187 part). *St. Catarina*: São Francisco do Sol: 1 yg. m. (USNM 71180 part). Florianopolis: 11 m., 7 f. (USNM 71188 part); end of Praia da Fora: 1 m., 1 f., 1 yg. (USNM 73445).

URUGUAY. Maldonado (near Montevideo): 19 m., 5 f. (MCZ 5926). La Sierra: HOLOTYPE of *U. uruguayensis*, m. (Torino). *Canelones*: Santa Lucia R.: 2 m. (USNM 72320).

ARGENTINA. Buenos Aires: Lavalle (Ajo): 6 m. (USNM 54716).

Uca (Celuca) crenulata (Lockington, 1877). (P. 232.)

U. (C.) crenulata coloradensis (Rathbun, 1893)

MEXICO. *Gulf of California*: *Sonora*: near mouth of Colorado R.: Horseshoe Bend: HOLOTYPE of *G. coloradensis*, m. (USNM 17459). Opposite mouth of "Hardy's Colorado R.": 31 m., 12 f. (USNM 18292); 3 m., 1 f. (MCZ 4263). Guaymas: 7 m., 4 f. (MCZ 5916).

U. (C.) crenulata crenulata (Lockington, 1877)

UNITED STATES. *California*: Newport Beach: 2 m. (NYZS). San Diego (Mission B.): 11 m., 1 f. (USNM 55220).

MEXICO. *Lower California (South District)*: west coast: Magdalena B. (Mangrove I.): 2 m. (AMNH 5477). Todos Santos B.: 35 m. + 1 extra claw, 9 f. (USNM 19033). *Gulf of California (South District)*: La Paz: type material of *G. gracilis*, 34 m., 6 f. (USNM 4622). Pichilinque B.: 22 m., 7 f. (USNM 22080). Head of Concepción B.: 7 m. (AMNH 5516). *(North District)*: San Luis Gonzaga B.: 4 m. (USNM 17458). San Felipe: 11 m., 2 f. (USNM 67725). *Sonora*: Guaymas: 13 m., 3 f. (MCZ 1594). *South of Gulf of California*: *Jalisco*: Tenacatita B.: 2 m., 1 f. (NYZS 381,151).

Uca (Celuca) speciosa (Ives, 1891). (P. 236.)

U. (C.) speciosa speciosa (Ives, 1891)

UNITED STATES. *Florida*: Miami: Key Biscayne: 6 m., 6 f. (NYZS); ditch by road to Tahiti Beach: 5 m., 4 (1 ovig.) f. (NYZS). Card Sound: 4 m., 2 f. (USNM 15256). Coon Key: 1 m. (USNM 73418). Key West: 3 m. (USNM 71290). Tortugas: 20 m., 7 f. (USNM 65942). Wakulla Beach: 1 m. (USNM 90606). Duck Rock (southwest coast): 1 yg. m. (AMNH 9622); 1 yg. f. (AMNH 9623). Sanibel I.: Heller's Cove or Clam Bayou: 2 m. (MCZ 10182). Sarasota B.: 1 m., 2 f. (USNM 42617); 6 m., 2 f. (USNM 73417). Manatee Co.: Sugarhouse Creek at Travertine Quarry: 4 m., 1 f. (USNM 71289).

WEST INDIES. *Cuba*: *Matanzas*: Hicacos Peninsula: Laguna Chaco, Xanadu: 8 m., 4 f. (USNM 99966). Laguna de Paso Malo Varadero: 3 m. (USNM 96456).

U. (C.) speciosa spinicarpa Rathbun, 1900

UNITED STATES. *Alabama*: near Mobile: 3 m., 1 f. (USNM 22312). Mobile: E. shore Cedar Pt.: 6 m., 1 f. (NYZS; gift of D. A. Archer, U. of Alabama, 1948). *Mississippi*: Biloxi B.: Ocean Springs: 3 m., 1 f. (USNM 10103). Biloxi: B. shore: 1 m. (USNM 21684). Biloxi: Ocean Springs Bridge: 3 m. (USNM 73419). Biloxi: 1 f. (USNM 54335). E. Biloxi below Back B. Bridge: 1 m., 1 f. (USNM 90305). *Texas*: Galveston: TYPES of *U. spinicarpa*, 2 m., 1 f. (USNM 22183); Offatt's Bayou: 1 m. (USNM 82110 part). Drain near Matagorda B. 1 m. (USNM 25034).

MEXICO. "Maron, Lagoon Madre, Mex. from oysters, saltwater—E. Palmer by purchase": 1 yg. f. (USNM 43364). Tampico: 1 m. (USNM 22311); 2 m. (USNM 43353 part).

Uca (Celuca) cumulanta Crane, 1943. (P. 240.)

WEST INDIES. *Jamaica*: Kingston Harbor: 1 m. (USNM 22313). *Curaçao*: 7 m., 1 f. (USNM 22310). Caracas B.: 1 m. (USNM 56909). *Trinidad*: near Port of Spain: Diego Martin: 53 m. (NYZS); Cocorite: 4 m. (NYZS); Lavantille: 5 m. (NYZS).

VENEZUELA. *Aragua*: Turiamo: 34 m., 12 f. (NYZS). *Delta Amacuro*: Pedernales: HOLOTYPE of *U. cumu-*

lanta, m. (NYZS 42423 = USNM 137402); PARATYPES, 7 m., 6 f. (NYZS 42423a = USNM 137403); 30 m., 20 f. (NYZS 42425 part; others listed by Crane 1943, now missing).

GUYANA. Georgetown: 13 m., 8 f. (NYZS).

BRAZIL. "Mamonguape stone reef": 1 m. (USNM 25700). *Rio de Janeiro*: Ilya Governador: 1 m. (USNM 73446). Paqueta: 1 m. (USNM 71182 part); 2 m., 1 f. (USNM 71171).

Uca (Celuca) batuenta Crane, 1941. (P. 244.)

COSTA RICA. Puntarenas: PARATYPES of *U. batuenta*, 2 m., 1 ovig. f. (NYZS 381,136 = USNM 79399); Ballenas B.: Additional PARATYPES, 4 m., 2 ovig. f., 1 extra claw (NYZS 381,137 = USNM 137404).

CANAL ZONE. Balboa (La Boca): HOLOTYPE of *U. batuenta*, m. (NYZS 4121 = USNM 137405); additional PARATYPES, 3 m. (NYZS 4122 = USNM 137406).

PANAMA. Near Old Panama: Abajo R. (near mouth by water pump): 1 m. (NYZS).

ECUADOR. Puerto Bolivar: 3 m. (NYZS).

Uca (Celuca) saltitanta Crane, 1941. (P. 247.)

COSTA RICA. Puntarenas: 3 m., 1 f. (NYZS 381,138).

CANAL ZONE. Balboa (La Boca): HOLOTYPE of *U. saltitanta*, m. (NYZS 4123 = USNM 137407); PARATYPES, 7 m., 7 f. (NYZS 4124 = USNM 137408); TOPOTYPES, 4 m., 4 f. (NYZS 4125 part = USNM 79403); 80 m., 50 (most ovig.) f. (NYZS 4125 part; others listed by Crane, 1941 now missing).

COLOMBIA. Buenaventura: several specimens identified with certainty but not preserved (Crane).

Uca (Celuca) oerstedi Rathbun, 1904. (P. 251.)

COSTA RICA. Punta Arenas: PARATYPE of *U. oerstedi*, 1 m. (USNM 31506).

CANAL ZONE. Balboa (La Boca): 9 m., 5 f. (NYZS 4119).

PANAMA. Old Panama: 6 m., 1 f. (NYZS 4120); west of Police Station: 44 m., 4 (3 ovig.) f. (NYZS).

Uca (Celuca) inaequalis Rathbun, 1935. (P. 254.)

NICARAGUA. Corinto: 2 m. (NYZS 381,139).

COSTA RICA. Puntarenas: 6 m., 3 f. (NYZS 381,140). Ballenas B.: 3 m., 1 f. (NYZS 381,141). Golfito: 10 m., 3 f. (NYZS 381,142).

CANAL ZONE. Balboa (La Boca): 10 m., 11 f. (NYZS 4126).

ECUADOR. Puerto Bolivar: 6 m., 3 f. (NYZS). Guayaquil: El Salado: TYPE of *U. inaequalis*, m. + 6 m., 3 f. (USNM 70833; locality spelled on records "Salada"); 1 m. (USNM 70900, "Salada"); 22 m., 10 f. (NYZS).

Uca (Celuca) tenuipedis Crane, 1941. (P. 258.)

COSTA RICA. Ballenas B.: HOLOTYPE of *U. tenuipedis*, m. (NYZS 381,143 = USNM 137409); PARATYPES, 8 m., 1 f. (NYZS 381,144, part = USNM 137410); PARATYPES, 1 f. (NYZS 381,144, part = USNM 79404).

Uca (Celuca) tomentosa Crane, 1941. (P. 261.)

EL SALVADOR. Los Blancos: holotype of *U. mertensi*, m. (Frankfurt, 1863).

COSTA RICA. Puntarenas: HOLOTYPE of *U. tomentosa*, m. (NYZS 381,132 = USNM 137411); PARATYPES, 3 f. (NYZS 381,133, part = USNM 137412); PARATYPE, 1 f. (NYZS 381,133, part = USNM 79406). Golfito: 1 m. (NYZS).

PANAMA. Near Old Panama: Abajo R. (near mouth by water pump): 3 yg. m., 3 yg. f. (NYZS).

Uca (Celuca) tallanica von Hagen, 1968. (P. 264.)

ECUADOR. Puerto Bolivar: 7 m. (NYZS).

PERU. Puerto Pizarro: HOLOTYPE of *U. tallanica*, m. (Leiden D 23046); PARATYPES, 5 m., 3 f. (Leiden D 23047).

Uca (Celuca) festae Nobili, 1902. (P. 267.)

EL SALVADOR. Puerto El Triunfo: holotype m. and paratypes, 2 m., of *Uca orthomana* (Frankfurt 1873 and 2074); 2 of paratypes of *Uca leptochela* (Frankfurt 2073 part). La Union: 3 m. (Frankfurt 2102).

PANAMA. Contreras I. (tide pool in jungle): 1 m. (AMNH 11562). Near Old Panama: Abajo R. (near mouth by water pump): 3 yg. m., 1 f. (NYZS).

ECUADOR. Guayaquil: El Salado: type material of *U. guayaquilensis*, 2 m., 1 f. (USNM 70831); 2 m., 1 f. (USNM 70901); 1 m., 2 ovig. f. (NYZS); El Rio: 48 m., 42 (8 ovig.) f. (NYZS). Rio Daule Inferiore: HOLOTYPE of *U. festae*, m. (Torino 1438). *El Oro*: Gualtaco (SW Ecuador): 4 m. (USNM 97908); 3 f. (USNM 97926).

Uca (Celuca) helleri Rathbun, 1902. (P. 271.)

GALAPAGOS IS. 1 yg. m., 1 yg. f. (USNM 63154). Albemarle I.: Black Bight: 1 m. (USNM 25666). Narborough I.: Mangrove Point: TYPE MATERIAL of *U. helleri*, 3 m., 1 f. (USNM 24829).

Uca (Celuca) leptochela Bott, 1954, 1958. (See p. 274.)

Uca (Celuca) dorotheae von Hagen, 1968. (P. 275.)

CANAL ZONE. Balboa (La Boca): 1 m., 1 f. (NYZS).

ECUADOR. Puerto Bolivar: 9 m., 3 f. (NYZS).

PERU. Puerto Pizarro: HOLOTYPE of *U. dorotheae*, m. (Leiden D 23054); PARATYPES, 25 m. & f. (Leiden D 23055).

Uca (Celuca) beebei Crane, 1941. (P. 278.)

NICARAGUA. Corinto: 2 m. (NYZS 381,148).

COSTA RICA. Puntarenas: 3 m. (USNM 32322; 46263); 2 m., 2 f. (NYZS 381,149). Boca del Rio Jesús Maria: 1 m. (USNM 32321).

PANAMA. Bahia Honda: 1 m. (NYZS 381,150). Panama City (Bellavista): 16 m., 6 f. (NYZS 4133). Old Panama: 7 m., 3 f. (NYZS 4134).

CANAL ZONE. Balboa (La Boca): HOLOTYPE of *U. beebei*, m. (NYZS 4129 = USNM 137413); PARATYPES, 8 m., 8 f. (NYZS 4130 = USNM 137414); 30 m., 19 f. (NYZS 4131 part); 2 m., 2 f. (NYZS 4131 part = USNM 79400); 5 yg. (NYZS 4132).

ECUADOR. Puerto Bolivar: 7 m., 1 f. (NYZS).

Uca (Celuca) stenodactylus (Milne-Edwards & Lucas, 1843). (P. 282.)

EL SALVADOR: *G. of Fonseca*: holotype of *G. gibbosus*, m. (MCZ 5911).

NICARAGUA. Corinto: 24 m., 7 f. + post-megalopal yg. (NYZS 381,145).

COSTA RICA. Port Parker: 1 m. (NYZS 381,146). Puntarenas: 3 m. (USNM 39098); 1 m. (USNM 46263). Golfito: 1 m. (NYZS 381,147). San Lucas: 2 m. (USNM 76133); 2 yg. m. (USNM 76140).

PANAMA. Agallero B.: Chitre: 1 m. (NYZS; gift of M. D. Burkenroad). Panama City: (Bellavista): 13 m. (NYZS 4128); 2 f. (NYZS).

CANAL ZONE. Balboa (La Boca): 1 m. (NYZS 4127).

ECUADOR. Puerto Bolivar: 3 m., 1 f. (NYZS).

CHILE. Valparaiso: TYPE-SPECIMEN of *G. stenodactylus*, m. (Paris).

Uca (Celuca) triangularis (A. Milne-Edwards, 1873). (P. 286.)

U. (C.) triangularis triangularis (A. Milne-Edwards, 1873)

MALAYSIA. *Labuan* [*North Borneo*]: 2 m. (NYZS; gift of Raffles).

INDONESIA. *Djawa* [*Java*]: Near Surabaja: Pasuruan: 10 m., 1 f. (NYZS); Trengglunga: 2 m. (NYZS). *Moluccas*: Amboina: 1 m. (Amsterdam); 1 m. (Leiden 1247); syntypes of *U. t. variabilis*, 3 m. (Leiden 1537). West Ceram: 1 m., 1 claw (Amsterdam).

NEW GUINEA. *West Irian*: Near Biak: Seroei-Japen: 5 m. (Leiden 724, part). *Territory of Papua and New Guinea*: near Madang on north-central coast: Maiwara: 6 m., 4 (1 ovig.) f. (NYZS).

? AUSTRALIA. "Great Barrier Reef Expedition": 5 yg. (BM 1950.12.1. 17-21; only record found that may be from Australia).

NEW CALEDONIA. "Nlle. Caledonie": TYPE of *G. triangularis*, 1 m. (Paris). Near Nouméa: 5 m., 5 f. (NYZS).

PHILIPPINES. *Sulu*: Tawi Tawi: 1 m. (NYZS). Joló (Princess Tarhata Kiram's Beach): 3 m. (NYZS). *Mindanao*: Zamboanga: 1 m. (USNM 43376); 1 m. (USNM 43454); north fishponds shorewards: 32 m. (NYZS). Gulf of Davao: Padada Beach: 2 m., 1 f. (AMNH 8305); 1 f. (AMNH 8306 part); 1 m. (AMNH 8312); 1 m. (AMNH 8314); 1 m. (AMNH 8315); 1 m. (AMNH 8316); 1 m., 1 f. (AMNH 8317); 1 m., 1 f. (AMNH 8336); Padada R. mouth: 1 m. (AMNH 8341); in and near Padada R. mouth: 2 m., 3 f. (AMNH 8383); 1 m., 1 f. (AMNH 8384); 2 m., 2 f. (AMNH 8385); Davao Beach: 9 m. (AMNH 8552). Mangrove swamp and adjacent muddy beach: 1 m. (AMNH 8553). Iling R., north of Sasa: 2 m. (NYZS). Madaum: 9 m., 1 f. (NYZS). *Negros Occ.*: Magnanod R., Victorias: 4 m. (USNM 73270). *Panay*: Jaro R.: 2 m. (USNM 73182). *Palawan*: Baheli R.: 4 m. (NYZS). *Luzon*: Mariveles: 1 m. (USNM 46652).

PALAU IS. 1 m. (Yokohama).

NANSEI [RYUKYU or LOO CHOO] IS. *Iriomote I.*: 1 m. (NYZS; gift of T. Sakai, U. of Yokohama).

U. (C.) triangularis bengali subsp. nov.

INDIA. Madras: 10 m. & f. + series of yg. (BM 92.7.15. 209-18). Karikal Marais: 1 m. (Paris 2-1946, part). Pondichéry: 1 m. (Torino 961).

BURMA. Mergui Archipelago: 2 m. (Amsterdam); 1 m. (Leiden 6).

MALAYSIA. *Malaya*: *Penang*: HOLOTYPE of *U. t. bengali*, m. (NYZS = USNM 137674); 49 m., 13 (1 ovig.) f. (NYZS); 1 m. (NYZS; gift of D. Tam); 2 m. (Leiden 1250); 2 m. (USNM 39172). Selangor: Port Swettenham: 1 m., 1 f. (NYZS; gift of M.W.F. Tweedie, Raffles).

Uca (Celuca) lactea (de Haan, 1835). (P. 292.)

U. (C.) lactea annulipes (Milne-Edwards, 1837)

ETHIOPIA. *Eritrea*: Massawa: 49 m., 18 f. (NYZS); 1 m. (AMNH 4323 part). Green I. (near Massawa): 4 m. (NYZS). Perim I.: 1 m. (Paris).

SOMALILAND. Obock: 2 m. (Paris).

KENYA. Near Mombasa: Gazia: Small series, including 3 m. checked (Paris).

"BRITISH EAST AFRICA": strait at Changamwe: 7 m., 4 f. (USNM 43379).

TANZANIA. *Pemba*: Near Chake Chake: Kiburunzi: 5 m. (NYZS). *Zanzibar*: 1 m. (USNM 19558); 5 m., 3 f. (USNM 22197). Chwaka: 2 m. (NYZS). Muongoni: 20 m. (NYZS). Chakwani Fish Ponds: 146 m., 22 f. (NYZS). Between Mbeni and Chakwani Fish Ponds: 3 m. (NYZS).

MOZAMBIQUE. *Inhaca I.*: east lagoon: 393 m., 90 (1 ovig.) f. (NYZS).

MADAGASCAR. 1 m. (Paris); northwest Madagascar: 1 m. (USNM 19554).

SOUTH AFRICA. *Natal*: Durban: 1 m. (AMNH 1153).

INDIAN OCEAN. "Mer des Indes": LECTOTYPE of *G. annulipes*, m., + 2 m., totaling 3 m. listed as "types non specifiés" by museum (Paris). *Mauritius*: 2 m. (BM); 1 m. (Paris). *Seychelles*: Mahé I.: 7 m. (BM 196).

PERSIAN GULF. 1 m. (Paris).

PAKISTAN. Kurrachee [? = Karachi]: 4 m. (USNM 13877). Karachi: 86 m., 19 (1 ovig.) f. (NYZS). Between Karachi and Clifton: 6 m., 1 f. (NYZS).

INDIA. Bombay: 2 m. (NYZS: identified in field; not saved). Mahé: 3 specimens (Torino). Ernakulam: 5 m., 2 f. (Marine Fisheries Lab., Ernakulam). Pondichéry: small series (Paris). Tuticorin: 5 m. (BM 90.10.20. 11-14). Karikal Marais: 1 m. (Paris). Madras: 2 m. (USNM 19710). Near Madras: Pamban: 32 m. examined in long series (BM Harding). "Calcutta": 1 m. (MCZ 5799).

CEYLON. 1 m. (BM 1.16.158). Negombo: 54 m. (NYZS).

BURMA. Rangoon: 3 m. (MCZ 5800). Mergui: 1 m., 1 f. (Amsterdam).

MALAYSIA. *Malaya*: *Penang*: 3 m. (NYZS); 1 m. (NYZS, gift of D. Tam, Bureau Fisheries). *Malacca*: Malacca: 3 m. (Leiden 1742): 3 m. (Amsterdam); 2 m. (USNM 39175 part). Port Dickson: 1 m. (Leiden 5240, part). Malacca Straits: 2 m. (Leiden 4891). *Labuan* [*North Borneo*]: 1 m. (NYZS; gift of Raffles through M.W.F. Tweedie).

SINGAPORE. 4 m. (NYZS; gift of Raffles through M.W.F. Tweedie). Gaylang R. by Kallong Airport: 49 m., 41 f. (NYZS).

"BORNEO." lectotype of *G. porcellanus*, m. and paratype m. (BM 901.444.106).

INDONESIA. *South China Sea*: Anambas Is.: Pulo Siantan: 1 m. (USNM 23365); Pulo Lankawi: 4 m. (USNM 23875). *Kalimantan* [*Borneo*]: Pontianak:

1 m. (Amsterdam). *Djawa* [*Java*]: Djakarta [Batavia] at Tanjong Priok: 5 m. (Leiden 2010, part); 7 m. (Leiden 2012); 7 m., not designated types, but labeled "*Gelasimus consobrinus* de Man," as stated on p. 298 (Amsterdam). North coast: 3 m. (Leiden 2031). Madura [Madoera]: 4 m. examined (Leiden 2035, part). Besuki [Besoeki]: 1 m. (Leiden 238, part). Bantam Pruput: 1 m. (USNM 43378). *Celebes*: Makasar [Makassar]: 2 m. (Leiden 2608); 1 m. (Leiden 5239); 29 m., 3 f. (MCZ 7247). Parepare: 10 m. (Amsterdam, part).

PHILIPPINE IS. *Sulu*: Tawi Tawi: 28 m. (NYZS). Tapiantana I.: 1 m. (USNM 43449). *Mindanao*: Sasa: Gulf of Davao: 6 m., 1 f. (NYZS). Davao: Malalag: 5 m. (NYZS). *Panay*: Iloilo: 8 m. (USNM 73198 part). *Samar*: Catbalogan: 3 m. (NYZS; gift of Sohrab Boya, Araneta Institute of Agriculture). *Palawan*: Ulugan B.: 1 m.; gonopod has some *l. perplexa* similarities (USNM 43450).

U. (*C.*) *lactea mjobergi* Rathbun, 1924

AUSTRALIA. *Northern Territory*: Darwin ("Buffalo Creek" and Dinah B.): 16 m., 28 f. (NYZS); Golf Club Creek: 23 m., 10 f. (NYZS). *Western Australia*: Broome: PARATYPE of *U. mjobergi*, m. (USNM 56418); 245 m., 5 f. (NYZS). Near Broome: Cape Boileau: 1 m., 1 f. (BM 1932.11.30. 166-168).

NEW GUINEA. *West Irian*: Bosnek: Mokmer, near Biak: 1 m. (Leiden); west of Bosnek: 3 m. (Leiden).

U. (*C.*) *lactea lactea* (de Haan, 1835)

HONG KONG. Kowloon (Castle Peak Area): 39 m., 10 (1 ovig.) f. (NYZS).

CHINA. "Chine": 2 m. (Paris). *Fukien*: Amoy: 2 m., 1 f. (BM 1935.3.19.7); 1 m. (Leiden 252); 3 m., 3 ovig. f. (USNM 61836). Tsimei: 4 m. (USNM 57827). Chin Bey: 2 m. (USNM 57045). Jau Ab: 1 m. (USNM 59166). Liuwutien: 3 m., 1 f. (USNM 61839).

TAIWAN [FORMOSA]. Tamsui: 45 m., 2 (1 ovig.) f. (NYZS). Shinchiku: 1 m. (USNM 55384).

JAPAN. LECTOTYPE of *G. lacteus*, m. (Leiden 254 part), + additional TYPE MATERIAL (Leiden 254 part); additional specimens (Leiden 1575). *Kyushu*: Kagoshima: 1 m. (USNM 48475). Miyazaki Prefecture: 1 m. (NYZS; gift of Kyushu U.). Fukuoka: Tatara R.: 6 m. (NYZS; gift of T. Sakai, U. of Yokohama). *Honshu*: Hiroshima Prefecture: Onomichi: 4 m. (USNM 43377).

U. (*C.*) *lactea perplexa* (Milne-Edwards, 1837)

INDIA. Pondichéry: small series (Paris).

MALAYSIA. *Malaya*: *Negri Sembilan* (near Sungei Dua ferry): 1 m., 2 f. (NYZS). *Malacca*: Port Dickson: 1 yg. m. (Leiden 5240); 2 m. (Leiden 5270 part); Malacca: 2 m. (USNM 39175 part). *Sarawak*: Santubong: 1 m. (BM 1900.12.1.22). *Labuan* [*North Borneo*]: 3 m. (Torino).

[See also under INDONESIA for other localities on Borneo.]

SINGAPORE. 1 m. (NYZS; gift of Raffles through M.W.F. Tweedie). Gaylang R. by Kallong Airport: 21 m., 19 f. (NYZS).

THAILAND. *G. of Siam*: Laem Ngop [Lem Ngob]: 2 m. (USNM 39713). *Chon Buri*: Bong Saen: 4 m. (USNM account no. 214063-2 parts). Bangpoo (near Bangkok): 2 m. (USNM 94420; lost by Crane after examination).

INDONESIA. *Kalimantan* [*Borneo*]: Pontianak: 2 m. (Amsterdam part). Samarinda: type of *U. annulipes* var. *orientalis*, 1 m. (Torino 1521). *Sumatera* [*Sumatra*]: Simeuleu [Simaloer]: 4 m. (Leiden 2084). Benkulen: 10 m. (USNM 75867). *Djawa* [*Java*]: "Javae": 2 m., listed by museum as "TYPES NON SPECIFIÉS" of *G. perplexus* (Paris). West coast: 1 m. (Leiden 2030). Djakarta [Batavia], at Tandjong Priok: 1 m. (Leiden 2010 part). Bantam Pruput: 1 m. (USNM 43378). Madura [Madoera]: 23 m. (Leiden 2032). Near Surabaja: Trengglunga: 1 m. (Amsterdam); 4 m., 1 f. (NYZS); Pasuruan: 1 m. (Amsterdam); 50 m., 23 f. (NYZS); Besuki [Besoeki]: 2 m. (Leiden 238 part). *Sulawesi* [*Celebes*]: Makasar [Makassar]: 4 m., 1 f. (USNM 39475); 1 m. (MCZ 7247 part). Parepare: 5 m. (Amsterdam, part). *Molucca Is.*: Batjan (off Halmahera): 1 m. (BM). Tawang I. (near Pahaji B., western Halmahera): 19 m., 1 f. (MCZ 11184). *Tenimber* [*Timorlaut*] *Is.*: 1 m. (BM). *Aru* [*Aroe, Arrou*] *Is.*: 1 m. (Paris). *Seram* [*W. Ceram*]: Piru [Piroe]: 2 m. (Amsterdam); 3 m., 1 f. (Amsterdam). Ambon [Amboina]: 1 m. (Amsterdam).

PHILIPPINE IS. *Sulu*: Tawi Tawi: 10 m. (NYZS). Joló: (Princess Tarhata Kiram's Beach): 10 m. (NYZS). Tapiantana I.: 1 m. (USNM 43449). *Mindanao*: Zamboanga (northeast fishponds, seaward of dikes): 161 m., 31 (7 ovig.) f. (NYZS). Gulf of Davao: Sasa: 7 m. (NYZS). Iling R. (north of Sasa): 3 m. (NYZS). Madaum: 3 m. (NYZS). Malalag: 3 m. (NYZS). Mataling R., Malabang: 25 m., 3 yg. f., + 12 extra claws and several bodies in poor condition (USNM 43382). *Cebu Channel*: Waiming: 2 m. (USNM 26201). *Negros Occ.*:

Bangi Bangi, Magnanod R.: 8 m. (USNM 64979); 1 m. (USNM 64986); 3 f. (USNM 64989); 3 f. (USNM 64990); 2 f. (USNM 65008). *Panay*: shore about Iloilo R.: 1 m. (USNM 43452). Iloilo: 20 m., 4 f. (USNM 73198 part). Jaro R.: 11 m. (USNM 73191); 2 m. (USNM 73199). *Guimares*: 1 m. (USNM 26202); Jordan R.: 6 m. (USNM 43453). *Palawan*: Puerto Princesa: 6 m., 3 (1 ovig.) f. (NYZS). Ulugan B.: 1 m. (USNM 43450). *Luzon*: Novatas, near Manila (mouth of Dagadagatan R.): 1 m. (NYZS). Bataan: Lamao: 23 m., 2 f. (NYZS; gift of Miss Beatrice Haygood, Araneta Institute of Agriculture). Mariveles: 25 m. (USNM 46649). Casaguran: 4 m. (USNM 43381).

NANSEI [RYUKYU or LOO CHOO] IS. "Loo Choo": 2 m. (BM 87.5). Ishigaki I.: mouth of Miyara R.: 4 m., 1 f. (NYZS; gift of T. Sakai, U. of Yokohama). Kume-jima (Loo Choo Is.): 2 major chelipeds (USNM 73260). Okinawa: Baten: 1 m. (NYZS; gift of T. Sakai, U. of Yokohama).

JAPAN. Tokaito Coast: Oho Sima: 1 m. (USNM 22287).

NEW GUINEA. *West Irian*: Kotabaru [Hollandia], Japen I., and Biak: series, m. & f. (Leiden, collections by H. B. Holthuis, years 1952-1955). *Territory Papua & New Guinea*: near Madang on north-central coast: Maiwara: 21 m., 3 f. (NYZS). Port Moresby: Taurama Beach: 1 m. (U. of Papua & New Guinea).

AUSTRALIA. *New South Wales*: Trial B.: 1 m. (Bishop 2484); 2 m. (USNM 64607).

NEW CALEDONIA. 2 m. (USNM 20300). Near Nouméa: 13 m., 6 f. (NYZS).

PACIFIC OCEAN. *Caroline Is.*: 1 m. (BM 98.11.1. 1-5). Lawi-Kondo: 5 m. (Bishop 4435). *Solomon Is.*: 2 m. (Paris). *New Hebrides*: Malle Kula: 2 m. (Paris). *Fiji Is.*: Viti Levu: Rewa (near mouth Wainibokasi R.): 9 m., 3 f. (NYZS). Suva: (Queen Elizabeth Drive and flat between town and seaplane base): 31 m., 10 f. (NYZS). Tavua: 19 m., 17 f. (NYZS). Kandavu Island: Tavuki: 12 m. (MCZ 5801). Bau I.: 1 f. (MCZ 5803). Lasema: 2 m. (MCZ 9080). Nukulau I.: 1 m. (MCZ 5802). *Friendly Is.* [*Tonga*]: Vavau: 5 m. (BM 1911.9.18. 27-29). *Samoan Is.*: 2 yg. m. (USNM 72522). Pago Pago: 1 m. (USNM 6587). Apia: 9 m., 1 ovig. f. (USNM 43380).

Uca (Celuca) leptodactyla Rathbun, 1898. (P. 304.)

MEXICO. 3 m., the basis for Guérin's manuscript name, *Gelasimus leptodactylus* (Phil. Acad. 9-2965).

WEST INDIES. *Bahamas*: New Providence: Nassau (near Fort Montague): TYPE MATERIAL of *U. leptodactyla*, 1 m., 1 f. (USNM 22315). Bimini: north of Lerner Marine Lab.: 3 m., 3 f. (USNM 91738). Turks I.: 1 m. (AMNH 2296). *Puerto Rico*. San Juan: San Antonio Bridge: 13 m., 9 f. (USNM 24546). *Tobago*: near Pigeon Point: 11 m., 3 f. (NYZS). Lagoon off Buccoo Reef: 7 m. (NYZS).

VENEZUELA. *Aragua*: Turiamo: 14 m., 9 f. (NYZS).

BRAZIL. *Pernambuco*: Recife [Pernambuco]: 14 m., 3 f. (USNM 40617); swamp before beginning of Olinda Causeway: 5 m., 5 f. (NYZS); ? Pernambuco: 12 m., 7 f. (USNM 40618); *Bahia*: São Salvador [Bahia]: Bahia de Todos Santos: 3 m., 3 f. (USNM 48297); Ilya Itaparica: 29 m. (NYZS); 80 m., 24 f. (NYZS). Porto Securo: 3 m., 1 f. (USNM 22189). Plataforma: 10 m., 3 f. (USNM 40616). *Rio de Janeiro*: 21 m., 10 f. (MCZ 5923); Guanabara B.: Paqueta I.: 10 m. (USNM 71183 part); 4 m., 1 f. (USNM 74484); 2 claws, 7 f. ? 2 yg. (USNM 71182); Ilya Governador: 1 m. (USNM 71185); Niterói [Nictheroy]: Conto do Rio: 1 m., 1 f. (USNM 74438). São Francisco: 1 f. (USNM 73490). *Rio de Janeiro* and *São Paulo*: Parahyba R.: 1 m. (USNM 25701). *São Paulo*: Santos: between canals 4 and 5 of estuary: 2 m., 2 f. (USNM 71187). São Sebastião: 1 m. (USNM 47850). *Parana*: Paranagua: 5 chelipeds (USNM 71184). *St. Catarina*: São Francisco: 3 m., 9 f. (USNM 71186); 13 m., 7 f. (USNM 71180); 1 f. (USNM 73490); 8 m., 11 f. (USNM 71179). Florianopolis: 1 m. (USNM 71188 part). Also from Brazil: Paiuny: Amarracão: 1 m. (USNM 48894). Maruim: 4 m. (USNM 22318).

Not Examined. Additional specimens at USNM from throughout the West Indies.

Uca (Celuca) limicola Crane, 1941. (P. 308.)

EL SALVADOR. El Zunzal: 2 m. (Frankfurt 1862, 1864).

COSTA RICA. Golfito: HOLOTYPE of *U. limicola*, m. (NYZS 381,152 = USNM 137415); PARATYPES, 17 m. & f. (NYZS 381,153 part = USNM 137416); 1 m., 1 f. (NYZS 381,153 part = USNM 79401); 1 m. (NYZS).

Uca (Celuca) deichmanni Rathbun, 1935. (P. 311.)

COSTA RICA. Port Parker: 9 m., 7 f. (NYZS 381,154). Piedra Blanca: 1 m. (NYZS 381,155). Uvita B.: 7

m., 5 f. (NYZS 381,156). Golfito: 10 m. (NYZS 381,157).

PANAMA. Bahia Honda: 1 m. (381,158). Shore of Panama: HOLOTYPE of *U. deichmanni*, m. (USNM 70832). Panama City: 7 m., 6 f. (NYZS 4142); (Bellavista): 1 m. (NYZS). Old Panama: 2 m., 2 f. (NYZS 4143); below Police Station: 2 m. (NYZS).

CANAL ZONE. Balboa (La Boca): 5 m. (NYZS 4141).

Uca (Celuca) musica Rathbun, 1914. (P. 314.)

U. (C.) musica terpsichores Crane, 1941

NICARAGUA. Corinto: 1 f. (NYZS 381,159).

COSTA RICA. Port Parker: 1 m., 3 f. (NYZS 381,160). Golfito: 4 m., 1 f. (NYZS 381,161).

PANAMA. Old Panama: 2 m. (NYZS 4146).

CANAL ZONE. Balboa (La Boca): HOLOTYPE of *U. terpsichores*, m. (NYZS 4144 = USNM 137417); PARATYPES, 1 m., 1 f. (NYZS 4145 part = USNM 79405); PARATYPES, 2 f. (NYZS 4145 part = USNM 137418).

ECUADOR. Jambeli I., near mouth of Guayas R.: 3 m. (NYZS).

U. (C.) musica musica Rathbun, 1914

MEXICO. *Lower California (South District)*: West Coast: Magdalena Bay: 1 m. (USNM 50632). Isla Margarita: 2 m. (USNM 95527). *Gulf of California*: 42 m., 3 f. (AMNH 2424). *(South District)*: La Paz: 6 m. (USNM 2294). Pichilinque B.: HOLOTYPE of *U. musica*, m. (USNM 22081). *Near Puertocito*: 10 m., 1 f. (USNM 106176). *(North District)*: San Felipe: 1 m., 1 f. (USNM 67733); 2 m., 2 f. (MCZ 9334). Tepoca B.: 1 f. (USNM 58112). *Sonora*: shore of Guaymas B.: 1 m. (USNM 31512). *Sinaloa*: Mazatlan: 2 m. (USNM 5054). *South of Gulf of California*: *Nayarit* [*Tepic Terr.*]: San Blas: 63 m., 7 f. (USNM 99755).

Uca (Celuca) latimanus (Rathbun, 1893.) (P. 319.)

MEXICO. *Gulf of California (South District)*: La Paz: TYPE of *G. latimanus*, m. (USNM 17500). *Sinaloa*: Escuinapa: 1 f. (USNM 60230). *Nayarit* [*Tepic Terr.*]: San Blas: 10 m. (USNM 99754). *Jalisco*: Tenacatita B.: 6 m. & f. (NYZS; specimens lost).

NICARAGUA. Corinto: 1 m., 1 f. (NYZS 381,163). San Juan del Sur: 1 m., 1 f. (NYZS 381,164).

COSTA RICA. Port Parker: 1 m., 1 f. (NYZS 381,165). Culebra B.: 1 m. (NYZS 381,166). Gulf of Dolce: Santo Domingo: 1 m. (USNM 19442). Golfito: 4 m., 4 f. (NYZS 381,167); 3 m. (NYZS).

PANAMA. Panama City: 3 m., 2 f. (NYZS 4148). Contreras I.: 1 m. (AMNH 11563).

CANAL ZONE. Balboa (La Boca): 24 m., 8 f. (NYZS 4147).

ECUADOR. Puerto Bolivar: 2 m. (NYZS).

Appendix B. Keys

INTRODUCTION

The following keys are regional and artificial, not phylogenetic. It would no doubt have been possible to make one mammoth key to the entire genus, but the phylogenetic aspects of this genus have, it is hoped, been covered in text, tables, and diagrams. On the other hand, a means of practical identification of species is essential in this confusing group; a single key, it seems, would have been only a tour de force of little pragmatic value. Therefore any phylogenetic order that appears in the keys is adventitious.

Because of the fragility of specimens, the frequent absence in collections of some important appendages, and the fact that half of every population is female, effort has been made to include several characters for each species. Nevertheless in most species the most conspicuous characters are on the major cheliped only, while the most reliable, with few exceptions, show on the gonopod. The characters on the latter appendage are omitted in the keys whenever feasible because of the inconvenience and sometimes difficulty of adequate examination; when they are used, an attempt is made to refer only to the more macroscopic characters. Most field workers are in the habit of carrying at least a x10 lens; this should be adequate to settle many dubious cases even on a mud flat. It goes without saying, however, that the keys are only a preliminary guide to be used in close association with figures, plates, diagnoses, and descriptions.

One difficulty in the construction of the keys has been the allometric character of many attributes—particularly the proportions of fingers to manus in the major cheliped. The characteristics affected by growth as well as secondary sexual characters should be kept in mind during use of the keys. The more obvious attributes in these two groups are as follows. In the young the major fingers are much shorter than in adults, while the entire major cheliped is proportionately short; the carapace is narrower in the young and has the orbits more oblique. In females the orbits are usually less oblique than in males, the ambulatory meri broader, the suborbital crenellations larger, and the tubercles on the ambulatories both larger and more numerous. Any reference in the keys to slender ambulatory meri or extremely oblique orbits, or to other primarily non-sexual characters, apply to both sexes unless otherwise specified; that is, there may still be slight differences between the sexes in the species concerned, but the character indicated is clearly applicable to both sexes in comparison with its expression in the alternate choice in the key.

When the words *palm*, *pollex*, *dactyl*, and *fingers* appear, those of the major cheliped are to be understood, unless the term *minor cheliped* or *small cheliped* is used; *minor cheliped* is reserved for the small cheliped of the male; *small* applies to both sexes or to the female.

Species recorded from highly questionable localities are not included in the regional keys concerned. An example is *tangeri*, which was recorded once from Brazil. Others are listed on pp. 326-27.

In first planning these keys I had hoped to include behavioral and ecological characters. Because of the unexpected extent of both variation and convergence that has emerged, the idea proved impractical. On the other hand, any worker staying for a time in one subregion can easily construct a serviceable and biologically enlightening key, including unmistakable attributes of habitat, waving display, and sound production. When such keys are available and biologists using *Uca* in various ways come to know their material in the field, the overlong alternates on some of the following pages will no longer, we may hope, seem necessary.

The Guide to Characters that follows gives references to illustrations of the principal characters employed in the keys.

Guide to Characters

(For location of characters on the crab, see Figs. 1-3; 42-44 and Table 13.)

Character	*Examples*	
	Figures	*Plates*
CARAPACE (DORSAL PART)		
Front		
Narrow	26 *A, E*	13 *F*, 19 *B*
Wider	26 *C, F*	15 *H*, 17 *F*, 25 *F*
Base moderately constricted	26 *A*	13 *F*
Base strongly constricted	26 *E*	19 *B*
Anterior margin distinct	26 *G*	–
Anterior margin obsolescent	26 *H*	–
Orbital Margin		
Scarcely oblique	24 *E, H*	3 *E*, 27 *E*
Strongly oblique	24 *J*	7 *A*, 22 *E*, 28 *A*
Antero-lateral Angles		
Acute and produced	24 *C*	7 *E*, 22 *A*
Rectangular	24 *H*	23 *A*
Antero-lateral Margins		
Short to absent	24 *C, J*	9 *E*; 22 *E*; 38 *E*
Long	24 *H, M*	5 *A*; 27 *A*
Curving gradually into dorso-laterals	–	23 *A*
Turning at an angle into dorso-laterals	–	34 *A*; 36 *A*
Dorso-lateral Margins		
Weak to absent	–	18 *E*
Well-marked	–	19 *A*
Tuberculate	–	21 *E, F*
Carapace Convexity		
Slight	25 *C*	–
Almost semi-cylindrical	25 *F*	–
ORBITAL REGION		
Eyebrows		
Lower margin absent	26 *A, E*	–
Lower margin present	26 *C, G*	–
Narrow	26 *C*	–
Broad	26 *G*	–
Suborbital Margin		
Rolled out	26 *A*	–
Erect	26 *D*	–
Crenellations small to absent (except usually externally)	26 *G*	–
Crenellations large	26 *H*	–
Floor of Orbit		
With tubercles	26 *A*	–
With a ridge or mound	26 *B*	–
Without elevations	26 *C*	–
Eye		
With a style or stylet	29 *C*	19 *E, F*; 20 *A, B*
Eye diameter greater than that of erected stalk	31 *A*	–
Eye diameter similar to that of erected stalk	31 *H*	–

Character	*Examples*	
	Figures	*Plates*
MAJOR CHELIPED		
Merus (Antero-lateral Margin)		
With distal tooth or teeth	–	14 *E*; 21 *E*
With row of tubercles	7 *A*	3 *E*; 21 *A*
With crest	10 *A*	18 *E*
Without large structures	5 *A*	22 *A*
Outer Manus		
Tubercles large	38 *A-W*; 39 *C*	5 *C*; 21 *G*
Tubercles small	39 *A*, *E*	12 *G*; 30 *C*
Upper part bent over, with ridge and adjacent groove	43 (nos. 17, 16)	30 *I*
Tubercles largest near dorsal margin	–	15 *C*
Tubercles largest near pollex base	–	14 *G*
With proximal projection	85 *Ca*	22 *C*
Palm		
Oblique tuberculate ridge strong	44 (no. 41); 39 *B*; 40 *C*	26 *H*
Oblique tuberculate ridge weak	39 *I*	23 *D*
Oblique tuberculate ridge obsolescent to absent	39 *G*	22 *D*
Proximal Ridge at Dactyl Base		
Parallel to distal ridge	44 (no. 32)	27 *D*; 30 *D*; 38 *H*
Diverging from distal ridge	–	24 *H*; 25 *D*
Beaded Edge above Carpal Cavity		
Present	44 (no. 27); 39 *H*	–
Short and weak to absent	39 *I*	–
Lower Proximal Palm		
With enlarged or patterned tubercles	49 *Ca*	–
With parallel ridges ("stridulating ridges")	49 *Aa*	–
Dactyl (Outer)		
With 2 long grooves	38 *E*, *G*	–
With 1 long groove	38 *A*, *C*	–
With no long grooves	38 *I*, *K*	–
Broad and flat	39 *C*	–
Pollex (Outer)		
Base with definite small depression	39 *A*	15 *I*
Base with broad, shallow depression	38 *I*	14 *G*
Base without a definite depression	38 *A*	16 *C*
Shape somewhat triangular, the base deep	–	33 *C*, *G*
Shape normal, the base not wider than adjacent part of dactyl	–	37 *C*
Supraventral keel present	42 (no. 6)	37 *C*
Conspicuous pits present	–	21 *C*
Gape		
Dactyl with subdistal hook-like projection	39 *G*	16 *D*
Pollex and dactyl with forceps-like tip	38 *A*, *B*	–
Pollex with triangular projection	42 (no. 61); 12 *B*, *BB*	10 *C*, *D*; 32 *G*, *H*; 33 *G*, *H*
Pollex with a subdistal outer crest	39 *E*	–
Pollex with a subdistal tooth in middle row	–	26 *H*; 27 *C*, *D*
MINOR OR SMALL CHELIPED		
Merus		
Posteriorly flattened, with special tubercles	51 *A*	–

Character	*Examples*	
	Figures	*Plates*
Gape		
Narrow	46 *A*, *I*	–
Broad	46 *L*, *M*	–
Serrations present	46 *B*, *K*	–
Serrations vestigial or absent	46 *G*, *L*, *N*	–
Enlarged teeth present	46 *E*, *P*	–
Enlarged teeth absent	46 *B*, *J*	–
Chela with Thick Distal Brushes	46 *H*	–
AMBULATORIES		
Merus		
With simple tubercles not raised on striae	52 *A*, *B*	–
Tubercles in rows raised on vertical striae	52 *C*, *D*	–
Segment slender	–	3 *E*; 24 *E*; 39 *A*
Segment broad or enlarged on 4th leg	–	2 *A*; 6 *A*
Dorsal margin almost straight on 4th leg	–	39 *A*
Dorsal margin convex on 4th leg	–	2 *A*
1st Ambulatory Anteriorly with Tubercles or a Ridge	49 *B*, *D*	–
Pile on Ventral Surface of Some Segments	–	25 *A*
GONOPOD		
Tip thick and blunt	56 *A*; 58 *A*	–
Tip a projecting tube	58 *H*	–
Tip with short, spinous projection	61 *G*, *I*	–
Flanges moderate to wide	58 *A*, *B*, *E*	–
Flanges vestigial to absent	58 *G*, *H*, *I*	–
Thumb large, subdistal	58 *D*, *E*, *F*	–
Thumb long	56 *F*; 58 *I*	–
Thumb arising far from tip	58 *B*	–
Thumb a nubbin	58 *H*	–
Thumb a straight shelf	71 *B*	–
Thumb an oblique shelf	71 *A*	–
Inner process large, truncate	58 *E*; 66 *B*	–
Inner process thin, tapering	58 *D*, *G*, *H*, *I*	–
Inner process tumid	58 *A*, 65 *B*	–
GONOPORE *(Female)*		
With tubercle or protuberance	54 *B*, *E*, *KK*	–
Without tubercle	54 *D*, *II*	–
ABDOMEN *(Male)*		
Segments all distinct	53 *A*	–
Some segments more or less fused	53 *C*, *D*	–
MAXILLIPEDS		
Spoon-tipped Setae on 2nd		
Each with a pointed basal process	37 *E*, *F*, *G*	–
None with a pointed basal process	37 except *E*, *F*, *G*	–
Gill on 3rd		
Large, with distinct books	82 *C*, *D*, *E*, *F*, *G*	–
Small to vestigial, without books	82 *H*, *I*	–

KEY TO THE GENERA OF OCYPODINAE

Eyes elongate, occupying most of ventral surface of eyestalks. Chelipeds very unequal in both sexes. Antennular flagella rudimentary, completely hidden beneath front. .... *Ocypode*

Eyes round, terminal on slender eyestalks. Male with 1 cheliped enormously enlarged; the other, and both chelipeds in female, are minute and similar to one another. Antennular flagella small, not hidden beneath front. .... *Uca* (p. 15)

KEY TO THE SUBGENERA OF *Uca*

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to, rarely, 1.5 times, basal breadth of erected eyestalk. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of eyestalk. 5

2(1). Suborbital margin rolled out, its crenellations very small to absent, except sometimes near outer angle; floor of orbit often with tubercles, a ridge or a mound; gill on 3rd maxilliped small to vestigial, without books. 3

Suborbital margin erect, its crenellations large; floor of orbit without any elevations; gill on 3rd maxilliped large, with distinct books in at least most individuals of a population. 4

3(2). Major merus without large structures on antero-dorsal margin; tubercles on outer manus large, usually largest near pollex base; pollex never with a ventral carina; ambulatory meri always with simple tubercles that are never raised on vertical striae; gonopod tip usually thick and blunt, rarely a projecting tube. .... *Deltuca* (Indo-Pacific; p. 21)

Major merus with an antero-dorsal crest; tubercles on outer manus moderate to small, always largest in dorsal half; pollex sometimes with a ventral carina; ambulatory meri sometimes with some tubercles on vertical striae; gonopod tip always a projecting tube. .... *Australuca* (Indo-Pacific; p. 62)

4(2). Lower margin of eyebrow present; base of front between eyestalks moderately constricted, its breadth more than equal to diameter of the erected stalk; tubercles of outer major manus enlarged only at pollex base; pollex without a ventral carina; spoon-tipped setae on 2nd maxilliped never with a pointed basal process; eye never with a distal style. .... *Thalassuca* (Indo-Pacific; p. 75)

Lower margin of eyebrow absent; base of front between eyes strongly constricted, its breadth much less than diameter of erected stalk; tubercles of outer manus enlarged subdorsally as well as at pollex base; pollex with a ventral carina; spoon-tipped setae always with a pointed basal process; eye on major side sometimes with a distal style, especially in young. .... *Uca* (America; p. 125)

5(1). Carapace largely covered with prominent tubercles; orbital floor with a large, spinous tubercle near inner corner; lower edge of eyebrow absent; spoon-tipped setae of 2nd maxilliped with a pointed basal process .... *Afruca* (Eastern Atlantic)*

Carapace practically smooth; orbital floor without elevations; lower edge of eyebrow present; spoon-tipped hairs without a pointed basal process. 6

6(5). Gill on 3rd maxilliped in most individuals large with many books; a small depression outside pollex base with definite boundaries; no beaded ridge on carpal cavity's upper margin; predactyl ridges diverging. .... *Amphiuca* (Indo-Pacific; p. 96)

Gill on 3rd maxilliped small to vestigial, never with books; any depression outside pollex base without definite boundaries; beaded ridge usually present along carpal cavity's upper margin. 7

7(6). Front moderately narrow, its breadth between eyestalk bases only about twice diameter of erected eyestalk at its base; eye diameter distinctly greater than that of adjacent stalk; carapace convexity slight. .... *Boboruca* (America; p. 109)

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* Recorded once from Brazil. A single species, *tangeri*.

Front broader, usually much broader, its breadth between eyestalk bases always more than twice basal breadth of erected eyestalk; eye diameter similar to that of adjacent stalk; carapace convexity moderate to semi-cylindrical. 8

8(7). Antero-lateral margins long (excepting in *pygmaea*), curving into dorso-laterals; pollex never with a ventral carina; 1st ambulatory on major side never with special armature anteriorly; gonopod never ending in a projecting tube; thumb always large, subdistal. .... *Minuca* (America; p. 154)

Antero-lateral margins short, or, if long, angling sharply into dorso-laterals; pollex sometimes with ventral carina; 1st ambulatory on major side often with special armature anteriorly; gonopod often ending in a projecting tube; thumb usually arising far from gonopod's corneous tip and often vestigial. .... *Celuca* (America; 2 spp. Indo-Pacific; p. 211)

REGIONAL KEYS

1. Key to the Species of *Uca* in East Africa and the Red Sea

(Guide to Characters: p. 616)

Note on distribution: All of the species except *U. tetragonon* occur in suitable habitats from Somaliland to Natal, including offshore islands; *tetragonon* has apparently not been reported in Africa south of Zanzibar. In addition, the ranges of *tetragonon*, *vocans*, *inversa* and *lactea* extend northward to various points on both coasts of the Red Sea. For Madagascar see Key 2.

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to, rarely 1.5 times, basal breadth of erected eyestalk. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of erected eyestalk. 4

2(1). A long, distinct furrow outside major dactyl; floor of orbit with a row of tubercles; suborbital crenellations small and indistinct; gonopod ending in a slender tube; female gonopore without a tubercle. .... *urvillei* (p. 58)

No long, distinct furrow outside major dactyl; no tubercles on floor of orbit; suborbital crenellations large & distinct; gonopod tip thick & blunt; female gonopore with or without a tubercle. 3

3(2). Major dactyl strikingly broad & flat; oblique ridge on palm high with large tubercles; small cheliped in both sexes with fingers much longer than manus. Female: no pile posteriorly on carapace sides; a large protuberance beside gonopore. .... *vocans* (p. 85)

Major dactyl of conventional shape; oblique ridge on palm low, the tubercles small & irregular; small cheliped in both sexes with fingers shorter than manus which is notably broad. Female: a patch of pile posteriorly on carapace sides; no protuberance beside gonopore. .... *tetragonon* (p. 77)

4(1). Major dactyl with a large distal tooth; major merus with a crest; gonopod with large flanges; in both sexes small cheliped unusually large & ambulatory meri without tuberculate striae. Female: gonopore neither depressed nor triangular, but with its postero-outer margin slightly raised. .... *inversa* (p. 105)

No large distal tooth on major dactyl; no crest on major merus; small cheliped of usual proportions; ambulatory meri always with some tuberculate striae. Female gonopore either depressed or triangular. 5

5(4). A triangular depression outside base of major pollex; oblique tuberculate ridge on palm moderate to low, predactyl ridges diverging; gonopod ending in a tube; ambulatory meri broad in both sexes. Female: middle ambulatories with meri having tubercules, not tuberculate striae, on lower, posterior surfaces which are bent forward; gonopore triangular. .... *chlorophthalmus* (p. 98)

No triangular depression outside base of major pollex; oblique tuberculate ridge on palm high; predactyl ridges parallel; gonopod ending in wide flanges; ambulatory meri narrow in both sexes. Female: tuberculation of middle ambulatory meri on vertical striae, the segments not bent; gonopore appearing deeply depressed, the marginal lip strongly tilted. .... *lactea* (p. 292)

2. Key to the Species of *Uca* in Madagascar, Pakistan, India, Ceylon, Burma, and Western Malaya

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to, rarely 1.5 times, basal breadth of erected eyestalk. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of erected eyestalk. 7

2(1). No long, distinct furrow outside major dactyl; suborbital crenellations large and distinct; no tubercles on floor of orbit; female chelae never with enlarged teeth in gape. 3

1 or 2 long distinct furrows outside major dactyl; suborbital crenellations small and indistinct; tubercles sometimes present on floor of orbit; female chelae usually with 1 or 2 enlarged teeth on at least 1 side. 4

3(2). Major dactyl strikingly broad & flat; oblique ridge on palm high with large tubercles; small cheliped in both sexes with fingers much longer than manus. Female: no pile posteriorly on carapace sides; a large protuberance beside gonopore. *Occurs throughout this key's area.* .... *vocans* (p. 85)

Major dactyl of conventional shape; oblique ridge on palm low, the tubercles small & irregular; small cheliped in both sexes with fingers shorter than manus, which is notably broad. Female: a patch of pile posteriorly on carapace sides; no protuberance beside gonopore. *Occurs throughout this key's area.* .... *tetragonon* (p. 77)

4(2). No row of tubercles on floor of orbit; 2 long furrows on major dactyl; gonopod with distinct flanges adjoining distal tube. Female: sometimes with antero-lateral margins practically absent but if so gonopore not triangular with highest point at postero-inner angle; 4th ambulatory merus sometimes edged posteriorly with pile. 5

One long furrow on major dactyl; gonopod without apparent flanges, the pore at end of a more or less projecting tube. Female: gonopore either triangular with highest point at postero-inner angle or a simple depression; 4th ambulatory merus never edged with pile. 6

5(4). Antero-lateral margins absent, strongly converging from angles; no isolated, subdistal tooth on major merus; several subdistal teeth on dactyl and pollex forming forceps-like tip; 4th ambulatory merus broad, its dorsal margin convex; gonopod tip without spinous projection. Female: no postero-ventral pile on 4th ambulatory merus. *Bay of Bengal.* .... *rosea* (p. 29)

Antero-lateral margins present, not strongly converging; an isolated, subdistal tooth on major merus, distinct from the small crest; merus of last ambulatory slender; gonopod tip with a short, spinous projection. Female: 4th ambulatory merus edged postero-ventrally with pile. *Bay of Bengal; ? Madagascar.* .... *dussumieri* (p. 32)

6(4). A row of tubercles on floor of orbit; distal tube of gonopod elongate; tip of chela without forceps-like, enlarged teeth; female gonopore a slight, simple depression. *Madagascar; Pakistan; western India.* .... *urvillei* (p. 58)

No row of tubercles on floor of orbit; distal tube of gonopod not elongate; tip of chela forceps-like; female gonopore partly rimmed, with highest point at postero-inner angle. *Bay of Bengal.* .... *forcipata* (p. 48)

7(1). Small chelipeds in both sexes with merus posteriorly flattened, armed with tubercles arranged in a supraventral row that curves up distally; orbits very oblique; gonopod tip tubular, greatly produced. *Bay of Bengal.* .... *triangularis* (p. 286)

Small chelipeds with merus not posteriorly flattened & not with a row of tubercles; orbits not strongly oblique; gonopod tip with or without flanges. 8

8(7). No oblique tuberculate ridge on palm; a crest on major merus; small chelae exceptionally large; postero-lateral striae absent; ambulatory meri without tuberculate striae. *Madagascar*; *Karachi, Pakistan.* .... *inversa* (p. 105)

Oblique tuberculate ridge on palm present; no crest on major merus; small chelae of usual size; ambulatory meri always with some tuberculate striae. 9

9(8). A small depression with definite margins outside base of major pollex; oblique tuberculate ridge on palm moderate to low; predactyl ridges diverging. Gonopod ending in a tube. Ambulatory meri broad in both sexes. Female: middle ambulatories with meri having tubercles, not tuberculate striae, on lower, posterior surfaces which are bent forward. *Indian Ocean*; *western Malaya.* .... *chlorophthalmus* (p. 98)

No definite depression outside base of major pollex; oblique tuberculate ridge on palm high; predactyl ridges parallel. Gonopod ending in wide flanges. Ambulatory meri narrow in both sexes. Female: tuberculation of middle ambulatory meri on vertical striae, the segments not bent. *Occurs throughout this key's area.* .... *lactea* (p. 292)

3. KEY TO THE SPECIES OF *UCA* IN MALAYSIA, INDONESIA, THAILAND, THE PHILIPPINES, NEW GUINEA, AND THE OCEANIC ISLANDS OF THE PACIFIC

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to, rarely 1.5 times, basal breadth of erected eyestalk. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of erected eyestalk. 10

2(1). No long, distinct furrow outside major dactyl; suborbital crenellations large & distinct; no tubercles on floor of orbit; female chelae never with enlarged teeth in gape. 3

1 or 2 long furrows outside major dactyl (sometimes faint); suborbital crenellations small & indistinct; tubercles sometimes present on orbit's floor; female chelae usually with at least 1 enlarged tooth on at least 1 side. 4

3(2). Major dactyl strikingly broad & flat; oblique ridge on palm high with large tubercles; small cheliped in both sexes with fingers much longer than manus. Female: no pile posteriorly on carapace sides; a large protuberance beside gonopore. *Range as in key title, east to Samoa.* .... *vocans* subspp. (p. 85; subspp. Table 3)

Major dactyl of conventional shape; oblique ridge on palm low, the tubercles small & irregular; small cheliped in both sexes with fingers shorter than manus, which is notably broad. Female: a patch of pile posteriorly on carapace sides; no protuberance beside gonopore. *Range as in key title, east to Tahiti.* .... *tetragonon* (p. 77)

4(2). Males & females with a row of distinct tubercles on orbital floor (excluding scattered, minute granules or a mound, found in *acuta*, below); a long lateral furrow on major dactyl present, but sometimes faint. 5

Males never, females in rare individuals only, with a row of tubercles on orbital floor; major dactyl with 1 or 2 long, distinct lateral furrows. 7

5(4). Row of orbital tubercles very long (up to 22; very rarely vestigial); lateral furrows on pollex & major dactyl often faint; no single, large tooth on either finger but a series of subdistal tubercles on each usually slightly enlarged; flanges present on gonopod, the anterior curving strongly & decreasing in height away from pore; female gonopore trapezoidal with a posterior tubercle and a low rim. *Philippines & Indonesia.* .... *demani* (p. 39)

Row of orbital tubercles shorter; 1 long, strong, lateral furrow at least on major dactyl; no flanges on gonopod; female gonopore with a postero-outer tubercle. 6

6(5). Major manus with outer tubercles very large, largest at pollex base; dactyl with a large, predistal, hook-like structure; pollex with tip slender & no triangular structure near its middle; gonopod tip only moderately produced; female cheliped with dactyl's dorsal margin nearly naked. *Sumatra to Fiji Is.*; *New Guinea*; *Philippines.* .... *coarctata* subspp. (p. 52)

Major manus with outer tubercles small, largest dorsally; pollex with a triangular projection beyond middle; no special structure on dactyl; tip of gonopod produced in a slender tube; female cheliped with dactyl's dorsal margin setose. *Nicobar Is.*; *Indonesia*; *western New Guinea*; *Philippines.* .... *bellator* (p. 64)

7(4). 2 long furrows on major dactyl; gonopod with distinct flanges. 8

1 long furrow on major dactyl; gonopod with or without distinct flanges. 9

(7). Antero-lateral margins absent, strongly converging from angles; no isolated, subdistal tooth on major merus; several subdistal teeth on major dactyl & pollex forming forceps-like tip; 4th ambulatory merus enlarged; gonopod tip always without spinous projection. Female: no postero-ventral pile on 4th ambulatory merus. *Western Malaya.* .... *rosea* (p. 29)

Antero-lateral margins present, not strongly converging; an isolated, subdistal tooth on major merus distinct from the small crest; no forceps-like tip on chela; 4th ambulatory merus slender, its dorsal margin practically straight; gonopod tip with or without a short, spinous projection. Female: 4th ambulatory merus edged postero-ventrally with pile. *Range as in key title, east to New Caledonia.* .... *dussumieri* subspp. (p. 32)

(7). Outer major manus with large tubercles; several subdistal teeth on major dactyl & pollex forming a strong forceps-like tip; no mound or minute granules on orbital floor; gonopod flanges vestigial, represented by struts each narrower distally than diameter of pore; female gonopore partly rimmed, with highest point at postero-inner angle. *Malaysia*; *Thailand*; *Indonesia*; *Philippines.* .... *forcipata* (p. 48)

Outer major manus with large tubercles only near pollex base; forceps-like tip on chela weak; a distinct mound on orbital floor near inner corner, sometimes with a scattering of granules nearby; gonopod flanges large; female gonopore with an outer tubercle. *Singapore*; *Sarawak.* .... *acuta rhizophorae* (p. 27)

10(1). Small chelipeds in both sexes with merus posteriorly flattened, armed with tubercles arranged in a supraventral row that curves up distally; orbits very oblique; gonopod tip tubular, greatly produced. *Range as in key title, east to New Caledonia.* .... *triangularis* subspp. (p. 286)

Small chelipeds with merus not posteriorly flattened and not with a row of tubercles; orbits not strongly oblique; gonopod tip with or without flanges. 11

11(10). A shallow, triangular depression outside pollex base; oblique, tuberculate ridge on palm moderate to low; 4th ambulatory merus broad, its dorsal margin convex; gonopod tip without flanges, tubular. Female: middle ambulatories with lower margins of meri bent forward. *Range as in key title, east to Marquesas* .... *chlorophthalmus crassipes* (p. 101)

No triangular depression outside pollex base; oblique, tuberculate ridge on palm strong; 4th ambulatory merus slender, its dorsal margin practically straight; gonopod tip with large flanges. Female: middle ambulatories not with bent lower margins of meri. *Range as in key title, east to Samoa.* .... *lactea* subspp. (p. 292; subspp. Table 6)

4. KEY TO THE SPECIES OF *Uca* IN AUSTRALIA

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to, rarely 1.5 times, basal breadth of erected eyestalk. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of erected eyestalk. *Tropical Australia.* .... *lactea* subspp. (p. 292; subspp. Table 6)

2(1). No long, distinct furrow outside major dactyl; suborbital crenellations large & distinct; no tubercles on floor of orbit; female chelae never with enlarged teeth in gape. 3

1 or 2 long furrows outside major dactyl (sometimes faint); suborbital crenellations small to absent; tubercles sometimes present

on orbit's floor; female chelae usually with at least 1 enlarged tooth on at least 1 side (female unknown in *demani australiae*). 4

3(2). Major dactyl strikingly broad & flat; oblique ridge on palm high with large tubercles; small cheliped in both sexes with fingers much longer than manus. Female: no pile posteriorly on carapace sides; a large protuberance beside gonopore. *Tropical & subtropical Australia.* ...... *vocans* subspp. (p. 85; subspp. Table 3)

Major dactyl of conventional shape; oblique ridge on palm low, the tubercles small & irregular; small cheliped in both sexes with fingers shorter than manus, which is notably broad. Female: a patch of pile posteriorly on carapace sides; no protuberance beside gonopore. *Tropical Australia: at least east coast.* .... *tetragonon* (p. 77)

4(2). Major dactyl with a long lateral furrow plus a subdorsal furrow about half or more dactyl's length; 4th ambulatory merus in female sometimes edged posteriorly with pile; gonopod flanges present. 5

Major dactyl with only one long furrow, the subdorsal furrow being proximal, short, sometimes vestigial; 4th ambulatory merus in female never edged posteriorly with pile; gonopod flanges absent, the tip tubular. 6

5(4). Poorly developed tubercles on orbital floor; major dactyl with subdorsal furrow about half dactyl's length; no single large tooth on dactyl or pollex, but a series of subdistal tubercles enlarged on each; 4th ambulatory merus moderately broad, its dorsal margin clearly convex; female unknown. Known from holotype only, *Broome.* .... *demani australiae* (p. 41)

No tubercles on orbital floor; major dactyl with subdorsal furrow long, traceable almost to tip; a tubercle usually slightly enlarged near pollex's middle, but no subdistal series on it or dactyl; 4th ambulatory merus slender, its dorsal margin straight &, in female of *d. dussumieri* only, edged postero-ventrally with pile. *Tropical Australia.* .... *dussumieri* subspp. (p. 32)

6(4). Major manus with outer tubercles large, largest at pollex base; dactyl usually with a predistal hook-like structure; pollex never with a large projection but always with a lateral groove; 4th ambulatory merus broad, the dorsal margin clearly convex; female cheliped with dactyl's dorsal margin nearly naked. *Tropical Australia.* .... *coarctata* subspp. (p. 52)

Major manus with outer tubercles small, largest near dorsal margin; dactyl never with a predistal hook-like structure; pollex always with a projection near middle, usually a large, tuberculate triangle, but sometimes a large tubercle; no pollex lateral groove; 4th ambulatory merus slender, the dorsal margin in middle almost straight; female cheliped with dactyl's dorsal margin conspicuously setose 7

7(6). Small cheliped in both sexes with large, triangular teeth, the opposing distal pair much the largest; major pollex with a long, low, triangular projection; female's 4th ambulatory carpus & manus with posterior patches of pile. *Tropical Australia.* .... *seismella* (p. 70)

Small cheliped with teeth not strikingly large & triangular, the largest never distal; projection on pollex occupying less than half its length; no pile on carpus & manus of female's 4th ambulatory. 8

8(7). Palm with oblique ridge high, the tubercles subregular; no depression outside pollex base; orbital floor with a row of tubercles (exception: *bellator longidigita*); gonopore rim raised or uneven; crab size small. *Tropical & subtropical Australia.* .... *bellator* subspp. (p. 64; subspp. Table 2)

Palm with oblique ridge low, the tubercles small & irregular; no tubercles on orbital floor; a faint depression outside pollex base; gonopore margin flat & smooth; crab size moderately large. *Tropical Australia.* .... *polita* (p. 72)

5. KEY TO THE SPECIES OF *Uca* IN HONG KONG, MAINLAND CHINA, NORTHWEST TAIWAN AND JAPAN

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to, rarely 1.5 times, basal breadth of erected eyestalk. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of eyestalk. 6

2(1). No long, distinct furrow outside major dactyl; pollex & major dactyl both flat; suborbital crenellations large & distinct; female chelae never with enlarged teeth in gape. 3

1 or 2 long furrows outside major dactyl (sometimes faint); suborbital crenellations small & indistinct; female chelae usually with 1 or 2 enlarged teeth on at least one side. 4

3(2). Major merus with a cluster of small tubercles distally on antero-distal margin; in both sexes orbits scarcely or not at all oblique and meri of 1st, 2nd, & 3rd ambulatories strikingly broad; dorsal margin of 4th convex in female. *Northwest Taiwan.* .... *formosensis* (p. 83)

Major merus with a large, sharp tooth distally on antero-dorsal margin; in both sexes orbits distinctly oblique & meri of ambulatories slender with dorsal margin of 4th straight. *Hong Kong, mainland China, & northwest Taiwan.* .... *vocans borealis* (p. 90)

4(2). 2 long furrows outside major dactyl; in both sexes merus of 4th ambulatory slender, its dorsal margin straight &, in female, edged postero-ventrally with pile; gonopod tip with a short, spinous projection. *Hong Kong & mainland China.* .... *dussumieri spinata* (p. 36)

1 long furrow outside major dactyl; in both sexes merus of 4th ambulatory broad, its dorsal margin convex; no short spinous or tuberculate projection on gonopod tip. 5

(4). Orbits almost straight, with antero-lateral margins long; 4th ambulatory with ventral margin clearly convex, in female not edged postero-ventrally with pile; gonopod with posterior flange large, anterior rudimentary; crab size large. *Range as in key title.* .... *arcuata* (p. 44)

Orbits oblique, with antero-lateral margins very short; 4th ambulatory with ventral margin almost straight, especially its distal half, & in female edged postero-ventrally with pile (often detached); gonopod with posterior flange small, anterior large; crab size small. *Hong Kong & mainland China.* .... *acuta acuta* (p. 25)

6(1). A shallow, triangular depression outside pollex base; oblique, tuberculate ridge on palm moderate to low; 4th ambulatory merus broad, its dorsal margin convex; gonopod tip without flanges, tubular; female's middle ambulatories with lower margins of meri bent forward. *Hong Kong.* .... *chlorophthalmus crassipes* (p. 101)

No triangular depression outside pollex base; oblique, tuberculate ridge on palm strong; 4th ambulatory merus slender, its dorsal margin straight; gonopod tip with large flanges; female's middle ambulatories not with bent lower margins of meri. *Range as in key title.* .... *lactea lactea* (p. 300)

6. KEY TO THE SPECIES OF *Uca* IN THE EASTERN PACIFIC

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to basal breadth of erected eyestalk, its distal portion slightly wider, spatuliform; tubercles of lower, outer manus large. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of erected eyestalk; tubercles of lower, outer manus moderate to minute. 6

2(1). Pollex covered with conspicuous pits & always clearly narrower than dactyl, which is broadest distal to middle; dorso-lateral margins of carapace & ventral margins of ambulatory meri with large separated tubercles or spines in female; at least traces of similar armature in male. 3

Pollex without pits (exception: *stylifera* with faint pits), subequal to or wider than dactyl which is broadest at or proximal to middle; no large separated tubercles on dorso-lateral margin (except sometimes a small one in female at posterior end) & none on ventral margins of ambulatory meri. 4

3(2). Major merus margined with large, separated tubercles antero-dorsally; male without large tubercles on dorso-lateral margins except for 1 at posterior end;

gonopod tip stout. Female with vertical lateral carapace margins granulate or tuberculate. *El Salvador—Peru (? Chile).* .... *maracoani insignis* (p. 147)

Major merus with a row of small, close-set tubercles & a single large, distal tooth; male with dorso-lateral margins more or less spinous. Female with vertical lateral margins vestigial, unarmed. *Central America to Peru.* .... *ornata* (p. 150)

4(2). Major merus with a large convex flange antero-dorsally; tip of gonopod thick, blunt; merus of 4th ambulatory in female with pile on postero-dorsal margin; female gonopore with a large tubercle. *Gulf of California to Peru.* .... *princeps* subspp. (p. 128)

Major merus with a low, straight-edged ridge ending distally in an abruptly higher tooth or small crest; tip of gonopod slender, tapering; merus of 4th ambulatory in female without pile on postero-dorsal margin; female gonopore without a large tubercle, its shape either crescentic or angular. 5

5(4). Male ocular stylet always present, much longer than cornea; major pollex faintly pitted; female chela with marginal setae short. *El Salvador to Peru.* .... *stylifera* (p. 140)

Male ocular stylet occasionally present, no longer than cornea; major pollex not pitted; female chela with marginal setae moderately long, stiff, close-set. *El Salvador to Ecuador.* .... *heteropleura* (p. 133)

6(1). Small chela: gape wide, in middle clearly wider than adjacent part of dactyl, usually much wider; opposing edges practically parallel at least in gape's proximal half & always with only the chela tips in contact; serrations absent or, rarely & maximally, few, minute & irregular, never in contact; carapace strongly arched. 7

Small chela: gape much narrower, ranging from about equal to width of adjacent part of dactyl to, in distal half, absent; serrations various; carapace arching various. 9

7(6). Eyebrow narrower than smaller dimension of adjacent part of depressed eyestalk; major pollex with a subdistal, tuberculate tooth or crest; proximal palm without a stridulating ridge; 3rd to 6th abdominal segments in male with traces only of fusion. *Costa Rica & Panama.* .... *deichmanni* (p. 311)

Eyebrow clearly wider than smaller dimension of eyestalk; major pollex distally tapering; proximal palm with or without a stridulating ridge; 3rd to 6th abdominal segments in male almost completely fused. 8

8(7). Major cheliped with fingers shorter than manus; no proximal stridulating ridge on palm, its oblique, tuberculate ridge obsolescent to absent; 1st major ambulatory without anterior tubercles; anterior margin of front distinct. *Lower California (La Paz) to Ecuador.* .... *latimanus* (p. 319)

Major cheliped with fingers long; oblique ridge & a proximal stridulating ridge on palm both present; 1st major ambulatory with anterior tubercles on merus & carpus; anterior margin of front obsolescent. *Subtropical & tropical eastern Pacific.* .... *musica* subspp. (p. 314)

9(6). Small chela ending distally in long, thick brushes of stiff setae; major outer manus with proximal end projecting beyond distal part of carpus; front broad, contained about 3 times in carapace breadth; antero-lateral angles acute, produced anteriorly. *El Salvador to Peru.* .... *panamensis* (p. 158)

Small chela not ending in thick brushes; no proximal projection on major manus; front when broad not with antero-lateral angles projecting strongly forward. 10

10(9). Small chela with gape moderate, about equal to width of adjacent part of dactyl or slightly less, the serrations weak, not in contact; front never very wide, being contained clearly more than 3 times in carapace breadth; oblique tuberculate ridge on palm always strong; pollex normally slender & tapering, little or not at all deeper proximally than adjacent part of dactyl, never conspicuously triangular. 11

Small chela with gape narrow, diminishing distally, the serrations usually strong and, in distal half, often in contact or nearly so; front, oblique tuberculate ridge on palm & shape of pollex various. 14

11(10). Antero-lateral margins divergent, long & strong; major manus with dorsal margin strong, set off from upper, outer manus by a distinct, adjacent groove; gonopod with a long thumb; female sometimes with pile on posterior sides of carapace. *Southern California & subtropical Mexico.* .... *crenulata* subspp. (p. 232)

Antero-lateral margins not divergent but short and usually poorly marked; major manus with dorsal margin indistinct, the adjacent groove absent or rudimentary; gonopod thumb various; female never with pile on posterior sides of carapace. 12

2(11). Orbits strongly oblique; major manus & triangle on proximal palm with minute tubercles in a reticulate pattern; gonopod thumb represented by a shelf. *Galapagos.* .... *helleri* (p. 271)

Orbits straight to scarcely oblique; tubercles on major manus & proximal palm not in a reticulate pattern. 13

3(12). 1st major ambulatory with anterior tubercles on merus, carpus, & manus; suborbital crenellations abruptly larger in both sexes near antero-lateral angle; gonopod thumb represented by a shelf. ...... *dorotheae* (p. 275)

No anterior tubercles on 1st major ambulatory; suborbital crenellations not abruptly larger near antero-lateral angle; gonopod thumb long. *El Salvador to Panama.* .... *limicola* (p. 308)

(10). Orbits extremely oblique; antero-lateral margins practically absent, with the dorso-laterals strongly convergent almost directly from antero-lateral angles; palm's oblique ridge absent. 15

Orbits little oblique (exception; moderately so in *zacae*); antero-lateral margins distinct, whether short or long; dorso-laterals variously convergent; palm's oblique ridge present or absent. 16

(14). Major cheliped with fingers clearly shorter than manus, which is not unusually tumid; center of palm smooth; 4th ambulatory merus broad, its dorsal margin convex; 1st ambulatory on both sides with anterior tubercles on carpus. *Costa Rica to Colombia.* .... *argillicola* (p. 220)

Major cheliped with dactyl subequal to manus which is strikingly tumid; center of palm coarsely tuberculate; merus of 4th ambulatory slender, its dorsal margin practically straight; 1st ambulatory without anterior tubercles. (Female unknown.) *Costa Rica to Colombia.* .... *pygmaea* (p. 161)

16(14). Suborbital crenellations in both sexes absent to minute, with no gradual increase in size toward outer angle; close to outer angle 1 or more large crenellations present or absent; crab size small to very small; pollex much deeper proximally than major dactyl's base & therefore appearing triangular (exception: *batuenta*); gonopod thumb a shelf. 17

Suborbital crenellations well developed at least in outer half where they increase gradually in size toward outer angle; crab size, pollex shape, & gonopod thumb various. 20

17(16). Major cheliped with pollex proximally subequal to adjacent part of dactyl; a large, triangular projection in pollex' distal third; branchial region without pile; suborbital margin in male without a large isolated tooth near outer angle; female ambulatories with pile at least on 2nd carpus dorso-posteriorly. *El Salvador to Peru.* .... *batuenta* (p. 244)

Major cheliped with pollex strikingly triangular, its proximal part being clearly wider than that of dactyl; pollex projection small or absent; rest of preceding characters various. 18

18(17). Carapace dorsally with at least 8 small patches of pile in both sexes (when abraded locations discernible through surface mounds or irregularities); 1st major ambulatory with anterior tubercles on merus & carpus; tubercles on palm's oblique ridge distally in a distinct row. *El Salvador to Peru.* .... *inaequalis* (p. 254)

No patches of pile on carapace; no anterior tubercles on 1st major ambulatory; tubercles on palm's oblique ridge distally obsolescent to entirely absent. 19

19(18). Major dactyl with 2 large, triangular projections; ambulatories of usual proportions, with dorsal margins of 2nd & 3rd meri slightly convex. *El Salvador to Colombia.* .... *saltitanta* (p. 247)

Major dactyl without projections; ambulatories in both sexes notably long & slender, with dorsal margins of meri straight. *Costa Rica & Peru.* .... *tenuipedis* (p. 258)

20(16). Front moderately narrow, contained 4 or more times in carapace breadth; gonopod flanges & thumb present or absent; thumb usually represented only by a shelf & always arising far down shaft; 1st major ambulatory with anterior tubercles present or absent. 21

Front wide, contained less than 3.5 times, usually less than 3, in carapace breadth; gonopod flanges and thumb always present, the thumb never represented by a shelf; 1st major ambulatory never with anterior tubercles. 29

21. Ambulatory meri very broad in both sexes, the middle ones with dorsal margins strongly convex; pile widespread dorsally on carapace, especially in females & young (caveat: sometimes largely abraded, persisting only in grooves), not confined to localized small patches; gonopod thumb present. 22

Ambulatory meri slender to moderate, the middle ones with dorsal margins at most slightly convex; pile when present confined to small patches in & near H-form depression, or to antero-dorsal region, or to postero-lateral region; gonopod thumb present or a shelf. 23

22. Crab size large; major carpus on inner side with a large tooth; palm's dorsal margin without a beaded edge or, if detectable, rudimentary & not curving downward; pile on ambulatories profuse, much of it persistent, especially in females & young; gonopod flanges present. *El Salvador to Panama.* .... *thayeri umbratila* (p. 113)

Crab size small; no large tooth on inner side of carpus but several minute tubercles present or absent; palm's dorsal margin with a strong beaded edge slanting downward along dorso-distal edge of carpal cavity; pile on ambulatories absent or practically so; gonopod flanges absent. *El Salvador to Peru.* .... *tomentosa* (p. 261)

23. Antero-lateral margins long & slightly to strongly diverging; no tubercles anteriorly on 1st ambulatory; no pilous depression outside pollex base; gonopod thumb present or a shelf. 24

Antero-lateral margins short & straight, concave, or converging; ambulatory tubercles & pollex base depression present or absent; gonopod thumb a shelf (exception: a nubbin in some specimens of *stenodactylus*). 25

24. Carapace dorsally with 2 to 6 patches of pile, conspicuous on branchial region; female without pile postero-laterally & on posterior sides; major chela short with pollex triangular, the pollex clearly broader proximally than dactyl base; no enlarged tubercles at gape base on outer manus; gonopod thumb a shelf. *El Salvador to Panama.* .... *oerstedi* (p. 251)

Carapace dorsally without pile in male; female with persistent pile postero-dorsally & posteriorly on sides; major cheliped with fingers strikingly long, ± 3 to 7 times manus length; a few enlarged tubercles on major manus outside gape base; gonopod thumb present, short. *El Salvador to Ecuador.* .... *festae* (p. 267)

25. Carapace dorsally in male usually with 6 curved patches of pile near middle, female with 2; pollex with a pilous depression outside base; 1st major ambulatory with anterior tubercles on carpus. *Ecuador & Peru.* .... *tallanica* (p. 264)

Carapace dorsally without pile or, at most, with traces in grooves; no pilous depression outside pollex base; anterior tubercles on 1st major ambulatory present or absent. 26

26. Palm with 2 predactyl ridges; small chela with serrations minute & similar; no longitudinal convexity on outer major manus. 27

Palm with only 1 predactyl ridge; small chela with serrations large & unequal (rarely worn or damaged in large specimens); a longitudinal convexity, broad & blunt, on outer major manus. 28

27. Gonopod with a protuberance on pore margin; 1st major ambulatory with anterior tubercles on merus distally, carpus & manus; female carapace without pile on sides posteriorly. *Panama to Peru.* .... *dorotheae* (p. 275)

Gonopod without a protuberance on pore margin (characteristics of 1st ambulatory unknown; female undescribed). *El Salvador.* .... *leptochela* (p. 274)

28. Tips of small chela obliquely truncate, meeting perfectly; 1st major ambulatory with tubercles anteriorly on carpus & manus; margins of middle ambulatory meri slightly convex in male; gonopod thumb an oblique shelf; female without pile on posterior sides of carapace. *Nicaragua to Peru.* .... *beebei* (p. 278)

Tips of small chela slender, pointed, not meeting perfectly; 1st major ambulatory with tubercles anteriorly on carpus only if at all; margins of middle ambulatory meri straight in male; gonopod thumb a transverse shelf or a nubbin; female with pile on posterior sides of carapace. *El Salvador to Peru (? Chile).* .... *stenodactylus* (p. 282)

29(20). Orbits oblique; antero-lateral margins short; dorso-laterals long & strongly converging; palm's oblique tuberculate ridge usually wholly absent, sometimes traceable through a few granules; female gonopore crescentic, its rim thickened externally but not unevenly raised, & without a tubercle. *El Salvador & Costa Rica.* .... *zacae* (p. 206)

Orbits little oblique to practically straight; antero-lateral margins long and convex; dorso-laterals short, little converging; palm's oblique tuberculate ridge vestigial (sometimes absent) to strong; female gonopore not crescentic. 30

0(29). Palm with oblique, tuberculate ridge vestigial, with apex low, to absent; pile in marbled pattern present over most of carapace dorsally (but often largely absent through abrasion); gonopod tip thickened by the large, truncate inner process; female gonopore with rim on three sides strong & unevenly raised. *Mexico to Peru.* .... *vocator ecuadoriensis* (p. 166)

Palm with oblique tuberculate ridge strong, the apex high; no pile dorsally on carapace; gonopod tip not appearing thick, the inner process being thin & tapering; female gonopore without a raised rim, but a marginal tubercle present or absent. 31

(30). Palm without a down-curving beaded edge from dorsal margin; proximal ridge at dactyl base diverging from adjacent groove; pollex gape with a row of enlarged, separated teeth in distal half but no subdistal tuberculate crest; ambulatory meri strikingly slender, even in female. *Lower California to Panama.* .... *brevifrons* (p. 180)

Palm with a strong down-curving beaded edge from dorsal margin; proximal ridge at dactyl base paralleling adjacent groove; no row of enlarged teeth on distal half of pollex gape but a subdistal tuberculate crest present on gape's outer edge. *El Salvador to Peru (? Chile).* .... *galapagensis* subspp. (p. 183)

7. Key to the Species of *Uca* in the Western Atlantic

(Guide to Characters: p. 616)

1. Front narrow: narrowest between eyestalk bases, its minimum breadth subequal to basal breadth of erected eyestalk, its distal portion slightly wider, spatuliform. Tubercles of lower, outer manus large. 2

Front wider: narrowest below eyestalk bases, its breadth between them twice or more basal breadth of erected eyestalk. Tubercles of lower, outer manus minute. 3

2(1). Major chela with fingers broad & flat, gape absent except proximally, dactyl widest in middle, pollex rough with pits; gonopod tip thick, its inner process tumid. Female without pile on 4th ambulatory carpus; chela with dactyl tip obliquely truncate. *Tropical Atlantic.* .... *m. maracoani* (p. 147)

Major chela with fingers tapering, in contact only distally, the gape normal; gonopod tip slender, tapering. Female with pile dorsally on 4th carpus; chela with dactyl tip pointed, its outer edge oblique but continuously convex, not truncate. *Tropical Atlantic.* .... *major* (p. 136)

3(1). Small chela: gape wide, in middle at least half width of adjacent part of dactyl, usually clearly more; opposing edges practically parallel in at least gape's proximal half & only the chela tips in contact; serrations absent or at most few, minute & irregular. Male abdomen with some segments partly fused. In both sexes 4th ambulatory merus slender, its dorsal margin straight. 4

Small chela: gape narrow, in middle clearly less than half width of adjacent part of dactyl, diminishing distally; opposing edges often almost in contact except near gape's base (exception: uncommon individuals of *pugilator* in Florida); serrations distinct & regular throughout middle section. Male abdomen with all segments distinct. 4th ambulatory merus various. 5

4(3). Major manus distal to carpal cavity without a strong, dorsal, tuberculate ridge and without an adjacent, pilous groove; 1st ambulatory in male without an anterior ridge on manus; female gonopore crescentic, the "horns" directed outward. *Tropical Atlantic south to southern Brazil.* .... *leptodactyla* (p. 304)

Major manus with a dorsal, tuberculate ridge and adjacent pilous groove running almost full length of subdorsal margin; 1st ambulatory in male with an anterior, supraventral ridge on manus on both sides; female gonopore not crescentic. *South Atlantic (Rio de Janeiro to Buenos Aires).* .... *uruguayensis* (p. 229)

5(3). No pile on ambulatories in either sex. 6
Ambulatory pile always present at least on 2nd & 3rd carpus & manus. (Exception: female *vocator*; see 10 below.) 8

6(5). Oblique tuberculate ridge on palm present; no lateral ridge on outer pollex; 1st major ambulatory with a row of anterior tubercles on carpus; gonopod tip tubular; flanges absent; 3rd & 4th ambulatory meri in female with margins convex; gonopore with marginal tubercle. *Tropical Atlantic.* .... *cumulanta* (p. 240)

No oblique tuberculate ridge on palm; outer pollex with a lateral ridge; no row of anterior tubercles on carpus of 1st major ambulatory; gonopod tip not tubular; 3rd & 4th ambulatory meri in female with margins straight; gonopore without a marginal tubercle. 7

7(6). Carapace practically semi-cylindrical; gonopod tip thick, contorted, with inner process distally broad and appearing fringed; female gonopore large, oval, rim raised except antero-internally. *Southern United States (Texas) & northeast Mexico.* .... *subcylindrica* (p. 209)

Carapace only moderately arched; gonopod tip not thick & contorted but relatively flat & narrow with 2 flanges & a tapering inner process; female gonopore not unusually large, without a raised rim. *Eastern & southern United States; Bahamas.* .... *pugilator* (p. 223)

8(5). Front narrow, contained at least 4.5 times in carapace breadth; palm with dorsal beaded edge above carpal cavity not curving down around cavity's distal margin. *Subtropical & tropical Atlantic.* .... *t. thayeri* (p. 114)

Front wider, contained at most 3.5 times in carapace breadth, usually less; downward degree of curving of palm's dorsal beaded edge various. 9

9(8). Antero-lateral margins practically straight, posteriorly always sharply angled; palm's dorsal beaded edge slanting only slightly downward, usually with little or no curvature; crab size small. *United States: south Florida & Gulf of Mexico; Mexico; Cuba.* .... *speciosa* subspp. (p. 236)

Antero-lateral margins convex, curving gradually into postero-dorsal margins; palm's dorsal beaded edge strong, curving distinctly downward along carpal cavity's upper distal edge. 10

10(9). Palm with oblique, tuberculate ridge vestigial to absent; pile in a marbled pattern present over most of carapace (but often largely absent through abrasion); 2nd & 3rd ambulatories without pile in females, present in males including on lower manus; gonopod tip thick, its inner process broad & truncate; female gonopore with edge unevenly raised, with 3 unequal tubercles. *Tropical north Atlantic.* .... *v. vocator* (p. 166)

Palm with oblique, tuberculate ridge always distinct (exception: atypical *mordax*, usually large), although the tubercles are often in irregular rows or bands; pile on carapace absent or scanty, confined to H-form depression, &, rarely, other grooves or antero-lateral region, never in a widely distributed marbled pattern; 2nd & 3rd ambulatories always with pile on carpus & manus in both sexes at least dorsally; gonopod with inner process narrow, tapering; female gonopore with edge raised or not & with or without a single tubercle. 11

11(10). 2nd & 3rd ambulatories with pile on ventral as well as dorsal sides of carpus & manus. 12

Pile completely absent on lower sides of ambulatories. 13

12(11). Major chela with proximal ridge at dactyl base paralleling adjacent furrow; eyebrow strongly inclined, almost vertical; pile on ventral sides of ambulatory carpus & manus scanty, fragile, confined to antero-ventral margins. *United States: northwest Florida to Texas.* .... *rapax longsignalis* (p. 197)

Major chela with proximal ridge at dactyl base clearly diverging upward from adjacent furrow; eyebrow moderately inclined; pile on ventral sides of ambulatory carpus & manus in both sexes thick, covering entire surface, persistent. *Tropical mainland Atlantic (Guatemala to the Amazon).* .... *mordax* (p. 173)

3(11). Proximal ridge at dactyl's base clearly diverging upward from adjacent groove, often either with an angle ventrally or with a curve throughout; center of palm always rough with tubercles of moderate size, not fine granules; pollex tip never with an outer subdistal crest but always with an enlarged, subdistal tubercle in gape's median row; meri of 2nd through 4th ambulatories slender, the dorsal & ventral margins of 4th straight in male, practically so in female; female gonopore without a tubercle but with the posterior part of edge clearly raised. *Subtropical & tropical Atlantic.* .... *burgersi* (p. 168)

Proximal ridge at dactyl's base straight, closely paralleling adjacent furrow, or (*minax* only) in upper portion minutely diverging from it; center of palm various; pollex tip always with an outer, subdistal crest at least indicated & never with an enlarged, subdistal tubercle in gape's median row; meri of ambulatories various; female gonopore various. 14

(13). Center of palm almost always finely granulate, usually appearing almost smooth, although exceptions occur; subdistal crest on outer pollex almost always strongly developed, the highest tubercle usually proximal with several others diminishing regularly toward tip; ambulatory meri broad, the dorsal margins of 3rd & 4th clearly convex at least on one side in both sexes; apex of oblique tuberculate ridge on palm high, the tubercles almost always continued little or not at all upward around carpal cavity; eyebrow only moderately inclined & usually narrower than smaller dimension of thickness of adjacent, depressed eyestalk; female gonopore with a tubercle. *Subtropical & tropical Atlantic.* .... *r. rapax* (p. 196)

Center of palm almost always with large tubercles that are sometimes flat; apex of oblique ridge low, often lower than its median section, the ridge continued or not upward around carpal cavity; crest on outer pollex tip highly variable within each species in strength & form; ambulatory meri slender in males, the dorsal margins of 4th scarcely or not at all convex, broader in females; eyebrow various; female gonopore with or without a small tubercle. 15

15(14). Front extremely broad, clearly more than one-third carapace breadth in both sexes; eyebrow wider than smaller dimension of adjacent, depressed eyestalk; oblique ridge inside palm not continued upward around carpal cavity; female carapace dorsally with antero-lateral patches of conspicuous tubercles; crab size large. *Eastern & southern United States.* .... *minax* (p. 176)

Front narrower, less than one-third carapace breadth in males, about one-third in females; eyebrow various; oblique ridge inside palm continued to variable extents upward around carpal cavity; female carapace dorsally without antero-lateral patches of tubercles or, at most, with a few small tubercles, highly variable; crab size small to moderate. 16

16(15). Eyebrow almost always strongly inclined, almost vertical, its breadth in males narrower than smaller dimension of adjacent, depressed eyestalk, in females subequal to it; front always with distal margin's inner edge normally rounded; female gonopore with posterior edge slightly raised and sometimes with a minute tubercle. *Eastern United States.* .... *p. pugnax* (p. 203)

Eyebrow weakly inclined, its breadth in males subequal to smaller dimension of adjacent, depressed eyestalk, in females broader; front with margin's inner edge often, but not always, appearing almost truncate in antero-dorsal view; female gonopore with edge entirely flat and without a tubercle. *Southern United States (Mississippi to Texas) & northern Mexico.* .... *pugnax virens* (p. 203)

Appendix C. Tables

TABLE 1
Characteristics of the Subgenera

	Deltuca	*Australuca*	*Thalassuca*	*Amphiuca*	*Boboruca*	*Afruca*	*Uca*	*Minuca*	*Celuca*
Range	Indo-Pacific →	→	→	→	America	Africa	America →	→	→ (plus 2 in Indo-Pacific)
No. of species	8	3	3	2	1	1	6	12	26
Front	Narrow →	→	→	Moderate →	→	→	Very narrow	Wide to very wide	Moderate to wide
Carapace convexity	Slight* →	→	→ *	Moderate	Slight	Moderate	Slight*	Moderate to great	Moderate to extreme
Eyebrows	Short; narrow; complete	Long; narrow to almost absent	Narrow to moderate; complete	Moderate; complete	Long; wide; complete	Moderate; lower edge absent →	→	Moderate to wide; complete →	→
Eye diameter compared with stalk	Markedly greater →	→	Scarcely greater →	→	Moderately greater	Scarcely greater →	→	Similar →	→
Suborbital margin	Rolled out →	→	Erect	Slightly rolled out	Erect →	→	→	→	→
Elevation(s) on orbital floor	Present or absent	Present	Absent →	→	→	Present	Absent →	→	→ **
Suborbital crenellations	Almost absent, except sometimes near angle →	→	Large	Absent or small except near angle	Moderate	Large	Moderate to large	Small except larger near angle	Almost absent to extremely large
Major merus Antero-dorsal margin: Armature	No large structures	Large distal crest	With or without a large tooth	With or without large crest	No large structures	Large distal tooth	Large structures	With or without moderate structure →	→
Major manus: Outer tubercles: General size	Large	Moderate to small	Large to moderate	Moderate	Small	Large	Large	Moderate or small (upper) & very small (lower)	Very small

TABLE 1 (*Continued*)
Characteristics of the Subgenera

	Deltuca	*Australuca*	*Thalassuca*	*Amphiuca*	*Boboruca*	*Afruca*	*Uca*	*Minuca*	*Celuca*
Major manus: Location of largest tubercles	Pollex base (usually)	Dorsally	Pollex base	Dorsally	→	Dorsally and near pollex base	→	Dorsally	→
Palm: Oblique ridge tubercles continue upward when present?	No	→	→	→	Yes	→	Usually	→	Usually (18 spp.; sometimes weakly)
Palm: Beaded ridge along upper carpal cavity?	No	→	→	→	Rudimentary	No	→	Yes (1 exception)	Usually (15 spp; sometimes weakly)
Palm: Carpal cavity continued distally?	Yes	→	→	Slightly	→	Yes	→	No (same exception)	Sometimes
Grooves on outer pollex and/or major dactyl	Present on both	Present on dactyl	Short on pollex; absent or trace on dactyl	Absent except for trace on dactyl	Absent	→	→	→	→ †
Pollex with ventral carina?	No	Sometimes	No	No	→	Yes	→	No	Sometimes
Gill on third maxilliped	Small to vestigial; no books	→	Large with books in many individuals	→	Vestigial	Large with books	→	Vestigial	Small to Vestigial

TABLE 1 (*Continued*)
Characteristics of the Subgenera

	Deltuca	*Australuca*	*Thalassuca*	*Amphiuca*	*Boboruca*	*Afruca*	*Uca*	*Minuca*	*Celuca*
Waving display (general type; moderate & high intensity)	Vertical	Vertical; semi-lateral trends	→	Semi-lateral	Lateral-straight	Lateral, straight & circular	→	→	→
Construction activities	Chimneys	None	None	Chimneys	Chimneys	None	None	Chimneys; rudimentary hoods	Chimneys (rare); pillars; hoods
Down-pointing included in threats	No	→	→	→	→	Yes	→	No	In one species
Special characters	Tubercles on ambulatory meri always simple	Gonopod tip always tubular	–	Depression outside pollex base; pre-dactyl ridges diverging	–	2nd maxilliped spoon-tips basally with spine	→ Eyes sometimes with styles	Antero-lateral margins long, curving behind (1 exception)	Palm-ambulatory armature in 13 spp.; gape sometimes wide; Dactyl crest in 5 spp.

*Except much stronger in one northern species or subspecies.
**Except for traces in *triangularis* subspp. & individual *lactea annulipes* females.
†Except for trace on pollex in individual *triangularis*.

TABLE 2

UCA BELLATOR: Principal Characteristics of the Subspecies

Characteristic		***bellator***	***longidigita***	***signata***	***minima***
General Range		*Philippines; East Indies*	*Near Brisbane, Australia*	*Tropical Queensland, Australia*	*Northwest Australia*
Gonopod:	Inner process	Straight; thick; appressed	Curved; appressed	Curved; appressed	Straight; slim; not appressed
	Thumb	Large; thick	Small	Absent	Absent
Gonopore:	Edge structure	Postero-external tubercle (moderate)	No tubercle, but external side of rim slightly raised	External tubercle (small)	Postero-external tubercle (moderate)
Orbital floor:	Tubercles or granules (both sexes)	Present	Absent	Present	Present in female; present or absent in male
Suborbital margin:	Crenellations (male)	Small, distinct, regular	Absent	Small, distinct, regular	Minute
Major merus:	Crest	Distally convex; tuberculate	Distally convex; weakly tuberculate or serrate	Straight, low, thick; tubercles irregular	Convex, large, smooth
Major pollex:	Ventral carina	Present	Absent	Present	Present
	Inner subdistal carina: tubercles or beading	Present	Present	Present	Absent
Minor chela:	1 pr. opposed, enlarged teeth near middle (adult male)	Present or absent	Present	Absent	Absent
Waving display:	Jerks present?	No	No	No	Yes

TABLE 3

UCA VOCANS: Principal Characteristics of the Subspecies

Characteristic		***borealis***	***pacificensis***	***dampieri***	***vomeris***	***hesperiae***	***vocans***	***Apparent Hybrids pacificensis x vomeris***	***Apparent Hybrids pacificensis x vocans***
General Range		*Hong Kong →Taiwan*	*Tropical west Pacific*	*Northwest Australia*	*East Australia & vicinity*	*East Africa, India, rarely →Singapore*	*Malaya →Nansei (Ryu Kyu) Is.*	*East New Guinea*	*South Philippines*
Gonopod:	Torsion	Absent	Slight	Moderate	Strong	Extreme	Extreme	Slight	Slight
	Inner process base tumid?	No	No	Yes	Yes	No	No	No	No
	Which flange broader?	Anterior	Anterior	Posterior (both narrow)	Posterior	Posterior (anterior minute)	Anterior	Anterior	Anterior
	Thumb very short?	No	No	Yes	No	Yes	No	No	No
	Anterior hollow	Absent	Absent	Absent	Moderate	Deep	Deep	Absent	Absent
Gonopore:	Posterior ridge	Moderate	Large	Large	Small	Minute→absent	Minute→absent	Large	Large
	Anterior ridge	Minute→absent	Minute→absent	Small	Large	Large	Large	Minute→absent	Minute→absent
Major manus:	Oblique ridge height	Low	High	High	High	High	High	High	High
	Outer tubercles	Large	Large	Moderate	Large	Large	Large	Large	Large
Major pollex:	2 projections sometimes present?	Yes, but weak	Yes	No	No	Yes	Yes	Yes	Yes
Major dactyl:	Notably deeper than pollex	Yes, in young	Yes	No	No	No	No	(Slightly)	(Slightly)
Carapace:	Dorso-lateral margins in adult male	Absent	Present	Absent	Absent	Weak→absent	Absent	Present, often short	Present, often short
Color:	Special pre-white phase?	No	Sometimes yellow	Blue spots	No	Sometimes yellow; often pale spots	Sometimes pale streaks	?	?
	Dactyl	Dull yellow→white	Violet→pink	Sometimes pink	Violet→pink (except yellow→white in New Guinea)	Yellow→white; rarely violet.	Yellow→white	?	?
Waving display:	Semi-lateral sometimes pronounced?	No	No	No (Maximally vertical)	No	Yes	No	?	?
	Seriality present?	No	No	Yes (high & medium intensities)	Sometimes (at medium intensity only)	No	No	?	?

TABLE 4

Comparison of Closely Related Forms in the Subgenus *UCA*

	m. maracoani *Atlantic*	***m. insignis*** *Pacific*	***ornata*** *Pacific*
Major merus with a row of long, separated tubercles	+	+	–
Major merus with small close-set tubercles and a large, distal tooth	–	–	+
Male: Postero-dorsal tubercles large only at margin's beginning & end	+	+	–
Male: Postero-dorsal tubercles large and separate*	–	–	+
Female: Postero-dorsal tubercles similar to those in male *maracoani*	+	–	–
Female: Postero-dorsal tubercles similar to those in male *ornata*	–	+	+
Female: Vertical lateral margins and their armature strong, not vestigial	+	+	–
Female: Strong tubercles across posterior carapace margin	–	–	+
Gonopod: not distally slender; inner process tumid	+	+	–
Gonopore: with tubercle large, depression deep	+	+	–

*One individual exception: see text.

TABLE 5

Geographic Distribution of Color Components in *UCA LACTEA* (Displaying males only)

KEY: Place names in *italics:* Component usual.
Place names in roman: Component occasional.
*Component present only in uncommon individuals suspected of being either *l. annulipes,* or hybrids between that subspecies and *l. perplexa.*
**Component present only in uncommon individuals suspected of being either *l. perplexa,* or hybrids between that subspecies and *l. annulipes.*

Color Components	***l. lactea***	***l. perplexa***	***l. annulipes***	***l. mjobergi***
Entire crab				
Polished white fully attained	*Taiwan*	Philippines	Singapore* *Pakistan*	—
Pale gray; pale buff; dull white	Hong Kong	*Philippines* New Guinea Fiji	Singapore East Africa (Massawa only)	N. W. Australia
Carapace: dorsal aspect				
Fine marbling: black and white; black and bluish; or brown and buff on white	—	Philippines *New Guinea* *New Caledonia* *Fiji* *Java*	*East Africa*	*N. W. Australia*
Transverse markings in bands or spots: black or blue on blue or white	—	Philippines** New Guinea (rare) (posterior band only)	*Sarawak* *Singapore* *Ceylon* *S. W. India* E. Africa (rare) (posterior bands only)	—
Major cheliped (often confined to outer manus)				
Polished white	*Hong Kong*	Java	Sarawak	—
Yellow present (buff to orange yellow)	Taiwan	*Philippines* *New Guinea* *New Caledonia* *Fiji* *Java*	Singapore*	N. W. Australia
Red present (pink to red)	—	Philippines**	*Sarawak* *Singapore* *Ceylon* *S. W. India* *E. Africa*	—
Anterior aspect: buccal & adjacent areas; minor chelipeds; ambulatories				
Yellow present	—	Philippines New Guinea *Fiji*	—	—
Red present (often on ambulatory meri only)	Hong Kong Taiwan	Philippines New Guinea New Caledonia	*Singapore* *Ceylon* *East Africa*	*N. W. Australia*

TABLE 6
UCA LACTEA: Principal Characteristics of the Subspecies*

	Characteristic	***mjobergi***	***annulipes***	***perplexa***	***lactea***
	General Range	*Northwest Australia*	*W. Africa to Singapore (occasionally to central Philippines)*	*Tropical W. Pacific (rarely to E. India)*	*Hong Kong to Japan*
Gonopod:	Torsion	Slight	Absent	Strong	Slight
	Which flange longer & broader?	Anterior	Anterior	Posterior	Posterior
	Pore in deep notch?	No	Yes	No	Yes
	Thumb reaching beyond flange base?	No	No	Yes	Yes
Gonopore:	Tilting of marginal lip	Slight	Great	Slight	Moderate
	Edge colored corneous brown?	Yes	No	Yes	Yes
Major pollex:	Outer row of tubercles	Absent	Prevalent only in S.W. & Central Africa	Rarely present, weak	Absent
	Supramarginal keel & groove	Absent	Usually present & strong in S. W. & Central Africa; elsewhere very variable	Absent in east; sometimes present in west	Usually present
	Predistal triangular tooth	Small or, usually, absent	Small to moderate (excl. zones of mingling with *perplexa;* there sometimes large)	Moderate to large (excl. zones of mingling with *annulipes;* there sometimes small)	Small or absent
Major dactyl:	Dorsal convexity	Throughout	Throughout	Distally only	Throughout
	Central portion wider than adjacent part of gape (excluding smallest adults)?	Yes, except in rare leptochelous individuals	No	Yes	No
Color:	Display white	Absent	Usually absent	Present or absent	Strongly present
	Outer manus: usual display color	Yellow	Pink or red	Yellow to chrome	White
Waving display:	Diminishing waves	Present	Absent	Absent	Absent
Structures:	Hoods observed?	No	In Karachi, Pakistan	In Madang, New Guinea (rare & rudimentary)	In N.W. Taiwan

*In order to facilitate comparison between *annulipes* and *perplexa,* which sometimes intermingle and apparently hybridize, the systematic order followed in the text is altered in this table. See discussion, p. 294.

TABLE 7
Probable Limits of Present Distribution in *UCA*

	Approx. N. Lat.	*Approx. S. Lat.*	*No. of Species*
Indo-Pacific Region			
Red Sea: Sinai Peninsula	28°	–	2
Southeast Africa: Umtata River	–	32°	2
West Australia: Monte Bello Is.	–	21°	2
East Australia: Sydney	–	34°	1
Japan: Fukuoka*	34°	–	2
Mid-Pacific: Marquesas Is.	–	10° (long. 140° W)	2
(Absent from Hawaii)			
American Region			
Northeast Pacific: southern California	34°	–	1
Southeast Pacific: at least to Zorritos, Peru; early records to Concepción and Valparaiso, Chile**	–	3°	2
Northwest Atlantic: Cape Cod at Provincetown†	42°	–	1
Southwest Atlantic: Buenos Aires, Argentina	–	35°	1
Galapagos Is.	0°	0°	3
Eastern Atlantic Region			
Northeast Atlantic: South Portugal	37°	–	1
Southeast Atlantic: Baia dos Tigres, Angola	–	16°	1
(Absent from Mediterranean Sea)			

*Formerly north to east coast of Honshu (35° N).

**Unconfirmed old records of three species near Valparaiso, Chile (33° S); records between 1950 and 1960 as far as Puerto Casma, Peru (10° S); distribution reviewed by von Hagen, 1968.2: 457ff.; see present study, p. 438).

†Formerly slightly north to Boston Harbor.

TABLE 8

Subregional Distribution of Species and Subspecies of *UCA:* Indo-Pacific Region

NOTE: Names in parentheses indicate the occasional occurrence of species or subspecies atypical of the region. Usually, they are found in scattered populations, as shown on the maps. In the case of the allopatric species *forcipata* and *coarctata,* which are shown coinciding in subregions 5 and 6, the populations are separate in the known examples. When on the contrary, different subspecies of *vocans* or *lactea* occur in the same subregion, local populations sometimes intermingle and there is morphological evidence of hybridization.

	1. N.W. Australia	2. China; N.W. Taiwan; Japan	3. Pacific Islands	4. E. Australia; New Caledonia	5. Ryukyus→ Philippines→E. Indies Axis; New Guinea	6. N. Borneo; N. Sumatra; Malaya→E. India	7. W. India; E. Africa
DELTUCA		*acuta acuta*				*acuta rhizophorae* *rosea*	
	dussumieri capricornis	*dussumieri spinata*		*dussumieri dussumieri*	*dussumieri dussumieri* (*d. spinata*)	*dussumieri spinata*	
	demani australiae				*demani typhoni* *demani demani*		
	coarctata flammula	*arcuata*	*coarctata coarctata*	*coarctata coarctata*	*coarctata coarctata* (*forcipata*) *coarctata flammula*	*forcipata* (*c. coarctata*)	*urvillei*
AUSTRALUCA	*bellator minima*			*bellator signata* *bellator longidigita*	*bellator bellator*	(*bellator bellator*)	
	seismella *polita*			*seismella* *polita*			
THALASSUCA			*tetragonon*	*tetragonon*	*tetragonon*	*tetragonon*	*tetragonon*
		formosensis					
	vocans dampieri	*vocans borealis*	*vocans pacificensis*	*vocans vomeris*	*vocans vocans* (*v. pacificensis*) (*v. vomeris*)	*vocans hesperiae* (*v. vocans*)	*vocans hesperiae*
AMPHIUCA		*chlorophthalmus crassipes*	*chlorophthalmus crassipes*	*chlorophthalmus crassipes*	*chlorophthalmus crassipes*	*chlorophthalmus crassipes*	*chlorophthalmus chlorophthalmus* *inversa inversa* *inversa sindensis*
CELUCA				*triangularis triangularis*	*triangularis triangularis*	*triangularis bengali*	
	lactea mjobergi	*lactea lactea*	*lactea perplexa*	*lactea perplexa*	*lactea perplexa* (*l. annulipes*)	*lactea annulipes* (*l. perplexa*)	*lactea annulipes*

TABLE 9

Subregional Distribution of Species and Subspecies of *UCA* Eastern Pacific and Western Atlantic Regions

	Eastern Pacific		Western Atlantic		
	1. S.W. U.S.A. and Mexico	2. Salvador→ N. Peru*	3. U.S.A.: (S. Florida)→ S. Brazil	4. U.S.A. and Mexico: Gulf of Mexico	5. U.S.A.: Massachusetts→ N. Florida
BOBORUCA		*thayeri umbratila*	*thayeri thayeri*		*thayeri thayeri*
UCA	*princeps monilifera*	*princeps princeps*			
		heteropleura	*major*		
		stylifera			
		maracoani insignis	*maracoani maracoani*		
		ornata			
MINUCA		*panamensis*			
		pygmaea			
		vocator ecuadoriensis	*vocator vocator*	*vocator vocator*	
			burgersi	*burgersi*	
	brevifrons	*brevifrons*	*mordax*	*minax*	*minax*
	galapagensis herradurensis	*galapagensis herradurensis*	*rapax rapax*	*rapax rapax*	
		galapagensis galapagensis			
				rapax longisignalis	
				pugnax virens	*pugnax pugnax*
		zacae			
				subcylindrica	
CELUCA		*argillicola*			
				pugilator	*pugilator*
	crenulata coloradensis				
	crenulata crenulata	*batuenta*	*speciosa speciosa*	*speciosa spinicarpa*	
			cumulanta		
			*uruguayensis***		
		saltitanta			
		oerstedi			
		inaequalis			
		tenuipedis			
		tomentosa			
		tallanica			
		festae			
		helleri			
		leptochela			
		dorotheae			
		beebei			
		stenodactylus			
		limicola	*leptodactyla*		
		deichmanni			
	musica musica	*musica terpsichores*			
		latimanus			

*[1] *U. maracoani insignis, macrodactylus* (name rejected), and *stenodactylus* were all described from Valparaiso, Chile, but not recently reported.

**[2] *U. uruquayensis* is known only from Rio de Janeiro, Brazil to Buenos Aires, Argentina.

TABLE 10
Biotopes of *UCA*

(See Figs. 21–23)

NOTE: Species and subspecies are omitted if their habitats are unknown or known only in general terms.

Subgenus	*Species and Subspecies*	*4. Stones with Sand, Shelly Conglomerate, or Coral Substrate (All with Some Mud)*	*5. Sand over Mud*	*6. Muddy Sand to Sandy Mud (Tide Levels: A, Upper; B, Lower)*	*8. Open Mud Flats near Stream Mouth*	*9. Muddy Sand to Mud with Partial Shade*	*11. Open Flats of Muddy Sand to Mud in Delta Lagoon*	*12. Muddy Stream Banks and Protected Flats, near Mouth, near Vegetation*	*13. Same as 12 but with Banks Steep*	*14. Same as 12 and 13, but Water Brackish*	*15. Upstream River Banks, Water Almost or Wholly Fresh*	*16. Subtropical and Temperate Marshes (Mangroves Absent)*
Deltuca	*acuta* subspp.							+	+			
	rosea							+	+			
	dussumieri subspp.							+				
	demani demani						+	+				
	arcuata							+	+			+
	forcipata							+	+	+		
	coarctata subspp.							+	+	+		
	urvillei				+			+				
Australuca	*bellator* subspp.							+		+	+	
	seismella							+	+			
	polita	+	+						+			
Thalassuca	*tetragonon*	+	+									
	vocans subspp.			+B	+							
Amphiuca	*chlorophthalmus crassipes*		+	+A			+	+				
	chlorophthalmus chlorophthalmus							+		+		
	inversa subspp.						+	+				
Boboruca	*thayeri* subspp.							+	+	+		
Afruca	*tangeri*	+	+	+A,B	+	+	+	+		+		+
Uca	*princeps princeps*			+B	+		+					
	heteropleura			+B	+							
	major			+B			+					
	stylifera			+A,B	+							
	maracoani				+	+	+	+				
	ornata				+	+	+	+				
Minuca	*panamenis*	+										
	pygmaea										+	
	vocator subspp.					+		+		+		
	burgersi					+	+	+				
	mordax						+	+		+	+	
	minax									+	+	+
	brevifrons									+	+	
	galapagensis subspp.						+	+		+		
	rapax			+A,B		+	+	+				
	pugnax			+A,B				+				+
	zacae					+		+		+	+	

TABLE 10 *(Continued)*

Subgenus	*Species and Subspecies*	*4. Stones with Sand, Shelly Conglomerate, or Coral Substrate (All with Some Mud)*	*5. Sand over Mud*	*6. Muddy Sand to Sandy Mud (Tide Levels: A, Upper; B, Lower)*	*8. Open Mud Flats near Stream Mouth*	*9. Muddy Sand to Mud with Partial Shade*	*11. Open Flats of Muddy Sand to Mud in Delta Lagoon*	*12. Muddy Stream Banks and Protected Flats, near Mouth, near Vegetation*	*13. Same as 12 but with Banks Steep*	*14. Same as 12 and 13, but Water Brackish*	*15. Upstream River Banks, Water Almost or Wholly Fresh*	*16. Subtropical and Temperate Marshes (Mangroves Absent)*
Celuca	*argillicola*									+	+	
	pugilator		+	+A,B								+
	uruguayensis					+		+				
	crenulata crenulata											+
	speciosa speciosa			+B		+						
	cumulanta						+	+				
	batuenta				+		+	+				
	saltitanta				+							
	oerstedi			+B				+				
	inaequalis					+	+	+				
	tenuipedis							+				
	tomentosa (after von Hagen)		+	+	+							
	tallanica				+	+						
	festae									+	+	
	dorotheae						+					
	beebei			+B	+	+	+	+		+		
	stenodactylus		+	+A			+					
	triangularis subspp.					+			+	+		
	lactea subspp.			+A		+	+	+		+		+
	leptodactyla	+	+	+A		+						
	limicola							+	+	+		
	deichmanni	+	+	+A								
	musica terpsichores			+A								
	latimanus					+	+	+		+		

TABLE 11

Variation of morphological characters in populations of *UCA RAPAX:* Mature males

NOTE: Individuals are counted as mature when, on the major cheliped, the dactyl is longer than the manus (that is, excluding pollex).

				Length/Breadth (%)		*Front/ Length (%)*		*Brow/Length (%)*	
Country	*Town*	*No. in Sample*	*Length Range (mm.)*	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*
U.S.A.	Miami	28	10–15	59–71	65.2	40.0–50.0	44.5	5.1–7.2	5.8
Puerto Rico	San Juan	65	10–15	55–69	65.0	36.0–49.0	42.7	4.4–6.6	5.4
Puerto Rico	Ponce	60	10–15	59–73	65.3	40.9–47.0	43.5	4.7–6.9	5.6
Virgin Is.	St. Thomas	51	10–13	61–69	64.7	37.3–45.0	40.0	4.7–6.2	5.4
Guatemala	Puerto Barrios	23	10–14	60–68	63.6	42.2–50.0	45.1	4.9–6.8	5.8
Venezuela	Maracaibo	103	10–18	55–74	64.6	35.0–48.0	40.4	4.0–6.6	5.6
Venezuela	Puerto Cabello	7	10–13	62–68	64.2	39.2–41.9	40.6	5.2–5.9	5.8
Trinidad, W.I.	Port-of-Spain	71	10–17	59–71	65.7	–	–	–	–
Guyana	Georgetown	21	10–16	58–68	63.4	38.6–46.4	42.1	4.8–6.6	5.5
Brazil	São Luiz	35	10–15	59–67	62.7	37.6–43.0	40.6	5.3–7.5	6.3
Brazil	Fortaleza	4	16–17	64–65	64.3	38.2–40.0	39.3	5.9–7.5	6.8
Brazil	Recife	7	10–14	61–72	66.1	38.4–44.8	41.7	5.4–6.4	6.0
Brazil	Bahía	4	11–13	61–65	62.5	41.6–41.8	41.7	5.5–6.8	5.9
Brazil	Río de Janeiro	71	10–17	58–70	64.5	35.0–45.0	39.6	5.1–8.4	6.1

TABLE 12

Distribution of Acoustic Components in *UCA*

KEY: +—Component present.
×—Component probable.
? —Presence of component questionable (observation or film record dubious)

Subgenus	Species	*Type of Data (Present Study)*						*Sound Produced by a Single Crab*													*Sound Produced by Contact Between Two Crabs*	
								Stridulation						*Vibration Against Carapace*		*Vibration Against Substrate*			*Sound Associated With Respiration*			
		Tape	*Heard in field (vibration detector)*	*Heard in crabbery/lab.*	*Film*	*Seen in field*	*Seen in crabbery/lab.*	*1. Major-merus-rub*	*2. Minor-merus-rub*	*3. Minor-claw-rub*	*4. Palm-leg-rub*	*5. Leg-wag*	*6. Leg-side-rub*	*7. Major-merus-drum*	*8. Minor-merus-drum*	*9. Major-manus-drum*	*10. Minor-chela-tap*	*11. Leg-Stamp*	*12. Bubbling*	*13. Membrane-vibration*	*14. Claw-rub*	*15. Claw-tap*
Deltuca	*acuta*				+	+						+										
	rosea				+	+						+	?									
	dussumieri	+	+		+	+	+	+				+				+		+			+	
	demani				+				+			?	?									
	arcuata				+			?														
	coarctata	+	+		+	+	+					+									+	
	urvillei				+	+		+				+		+				?			+	+
Australuca	*bellator*				+	+	+	+				+	+									
	seismella				+	+			+			+		+								
	polita				+	+		+														
Thalassuca	*tetragonon*	+	+		+	+		+				+									+	
	vocans	+	+		+	+		+				+									+	
Amphiuca	*chlorophthalmus*				+							+										+
	inversa				+							+										+
Boboruca	*thayeri*		+	+																		
Afruca	*tangeri*				+	+						+	+	+		+		+			+	
Uca	*major*					+		+														
	heteropleura				+							+										
	maracoani	+	+	+	+							+						+			+	
	ornata				+			+				+					+	+			+	
Minuca	*panamensis*															×						
	vocator	+	+	+	+	+	+									+				+		
	burgersi	+	+	+		+	+												+			
	mordax																					
	minax																					
	galapagensis				+			+	+			+										
	rapax	+	+	+	+	+	+					+						+			+	+
	pugnax		+		+	+	+					+						+			+	+
Celuca	*pugilator*		+		+	+		+			×	+				+		+			+	+
	uruguayensis										×											
	speciosa				+	+		?								+						
	cumulanta	+	+	+	+	+	+			?		+		+		+						+
	batuenta				+	+			+			+		+		?						
	saltitanta				+	+						+				?						
	oerstedi				+	+					?	+		+								
	inaequalis				+	+		+	+		+	+		+		?						
	festae					+		?	?			+		?								
	beebei				+	+			+		×	+			?							
	stenodactylus				+				+		×	+			?							
	triangularis	+	+																			
	lactea	+	+		+	+		+				+		+		+	+	?			+	+
	limicola				+	+						+										
	leptodactyla																					
	deichmanni				+	+		+		+	+	+		+		?	+				+	
	musica										×											
	latimanus				+			+	+	?		+										

Remarks	*Locality*	*References*	
		Previously Published	*Page No. (Systematic Section)*
	Singapore	–	28
	Malaya	–	30
5. Incl. rubbing against minor cheliped	Philippines, N. Caledonia	Crane, '66	34
5. Incl. rubbing against minor cheliped	Philippines	–	42
	Taiwan	–	46
	N. W. Australia, Fiji	Crane, '66	54
	Zanzibar	–	60
	Java, Philippines	–	67
	N. W. Australia	–	71
	N. W. Australia	–	73
	Red Sea, Zanzibar	Crane, '66	79
1. With circling motion	Red Sea, N. Caledonia, Fiji	Crane, '66	88
	Zanzibar	–	100
	Zanzibar, W. Pakistan	–	106
	Trinidad	von Hagen, '68.1	113
	Spain, Portugal, Angola	Altevogt, '59, '64; von Hagen, '62	121
	Trinidad	von Hagen, '68.1	137
	Panama (Pacific)	–	135
	Trinidad	Crane, '66; von Hagen, '68.1	146
	Panama (Pacific)	–	152
9. Inferred only from morphology	Panama (Pacific)	–	159
9. Synchronized with long roll	Trinidad	Crane, '66; von Hagen, '68.1; '70.3	165
	Trinidad, St. Thomas, Florida	von Hagen, '68.1; Salmon, '67	171
	Trinidad	von Hagen, '68.1	—
	East coast, U.S.A.	Salmon, '65	—
	Costa Rica	–	185
	U.S.A., W. Indies, Brazil	Crane, '66; Salmon, '67; Salmon & Atsaides, '68.1,2; von Hagen, '	194
	U.S.A., (east & Gulf coasts)	Salmon, '65, '67; Salmon & Atsaides, '68.1,2.	202
4. Inferred only from morphology	U.S.A. (east & Gulf coasts)	Early refs.: see, p. 480 Salmon & Stout, '62; Salmon, '65; Salmon & Atsaides, '68.2	225
4. Inferred only from morphology	Uruguay	–	229
	U.S.A. (Florida)	Salmon, '67; Salmon & Atsaides, '68.2	238
	Trinidad	Crane, '66; von Hagen, '68.1	241
	Panama (Pacific)	–	246
	Panama (Pacific)	–	249
	Panama (Pacific)	–	253
	Panama (Pacific)	–	256
	Ecuador	–	269
4. Inferred only from morphology	Panama (Pacific)	–	280
4. Inferred only from morphology	Panama (Pacific)	–	284
	N. Caledonia	–	289
	E. Africa; S.E. Asia; Taiwan; Fiji	Crane, '66	296
	Panama (Pacific)	Crane, '66	309
	Trinidad	von Hagen, '68.1	306
1. Performed antiphonally by 2 males	Panama (Pacific)	–	313
4. Inferred only from morphology	E. Pacific	Specializations pointed out first by Rathbun, 1914	314
	Costa Rica (Pacific)	–	321

TABLE 13

Organization of 84 Structures on *UCA* Claws and Their Relation to Ritualized Combat

Area (*Figs.* 42, 43, 44)	*Structure No.*	*Structure Name*	*Type of Variation*	*Range of Variation*	*Combat Components Using Structure* (*cf. Table 14*)	*Structure No.*
OUTER MANUS *Ventral Margin:*						
Length (plus any continuation on ventral pollex margin)	1	Enlarged tubercles	a. Occurrence b. Size c. Location of largest d. Distal end of row e. Arrangement f. Location of Keel	Present or absent Small to moderate Proximally or near pollex base Between pollex base and tip Tubercles usually in single line; rarely multiple, sometimes on low keel Full length, proximal or distal	Pollex-under-&-over slide Subdactyl-&-subpollex-slide Upper-&-lower-manus-rub Dactyl-submanus-slide	1
	2	Furrow beside tubercles on outer side	a. Occurrence b. Extent c. Depth	Present or absent Full length, proximal or distal Slight to moderate	Pollex-under-&-over-slide Dactyl-submanus-slide	2
Outer Surface:						
A. Entire region	3	Tubercles (excluding local specializations)	a. Size, general b. Size, regional c. Homogeneity d. Arrangement	Minute to small Ventral to dorsal size differences Rarely of different sizes in same region Rarely in reticulated pattern	Manus-rub Heel-&-hollow Heel-&-ridge Supraheel-rub (vertical)	3
B. ± Ventral half	4	Convexity of heel (= proximal ventral surface)	Range	Slight to moderate	Heel-&-hollow Heel-&-ridge	4
C. Pollex base	5	Depression	a. Size b. Tuberculation	Large, shallow and indefinite to small, deeper and distinctly bounded Present or absent, thick or sparse, similar or different in size from those of adjacent manus	Pollex-base-rub	5
	6	Keel below depression	a. Occurrence b. Extent proximally c. Extent distally d. Tuberculation	Present or absent Sometimes proximally to mid-manus; at least as row of tubercles From proximal part of pollex almost to tip Present or absent	Pollex-rub Pollex-base-rub	6
D. Cuff (= vertical convexity beside dactyl base)	7	Groove	Occurrence	Present or absent	Interlace	7
	8	Tubercles	Occurrence & arrangement	Linear to scattered to absent	Interlace	8
E. Central portion	9	Special longitudinal convexity	Occurrence	Rarely present	(Unknown)	9
	10	Tubercles	Size near gape	Sometimes abruptly larger	Interlace Pregape-rub	10

F. ± Upper third	11	Inward bending of surface	Degree	Slight to pronounced	Upper-&-lower-manus-rub: some or all, 11-24-(+1)	11
	12	Flattening of submarginal area	a. Degree b. Location of maximum	Absent to pronounced Throughout manus length or pronounced proximally, minimal to absent distally	↓	12
	13	Tubercles: proximal specializations	a. Occurrence b. Arrangement	Present or absent Vertical or oblique rows, reticulations, and/or rugosities		13
	14	Tubercles: submarginal specializations	a. Occurrence b. Size (cf'd. #3b) c. Arrangement	Present or absent Secondarily reduced As in 13b		14
	15	Submarginal longitudinal ridge	Occurrence	Rarely present		15
	16	Submarginal longitudinal smooth area	Occurrence	Present or absent		16
	17	Submarginal groove	a. Occurrence b. Extent c. Distinctness	Present or absent Throughout or proximal only Wellmarked to faint	(Also 17: Guide to heel in heel-&-ridge)	17
Dorsal Margin:						
A. Proximal part (coincides with upper edge of carpal cavity)	18	Beaded edge (see also #27)	a. Distinctness b. Extent	Beading strong or weak Distinct throughout or proximally only		18
B. Distal part	19	Breadth	Degree	Narrow to wide		19
	20	Flattening	Degree	Absent to strong		20
	21	Inward tilt	Occurrence	Present or absent		21
	22	Armature of outer edge	a. Distinctness b. Extent	Whether marked by a ridge and/or tubercles Edge distinct throughout or proximally only		22
	23	Armature of marginal surface	a. Occurrence b. Tubercles unpatterned c. Tubercles in rows d. Tubercles in reticulations e. Rugosities	Roughness of some kind(s) present or absent; form range b – e Crowded to very sparse, surface being otherwise smooth Transverse and/or oblique, slanted proximo-externally Size of smooth spaces Degree of tuberculation		23
	24	Demarcation between margin and upper palm	Occurrence	Present or absent		24